

# DEVONIAN SCHIZOPHORIID BRACHIOPODS FROM WESTERN EUROPE

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**ABSTRACT.** Six species and one subspecies of the genus *Schizophoria* are described from the Devonian of western Europe, with their stratigraphical ranges and postulated phylogeny. All taxa are shown to be externally and internally distinct. Neotypes are proposed for *Schizophoria provulvaria* (Maurer) and *S. strigosa* (Sowerby).

**SPECIMENS** of *Schizophoria* have been studied in this work from the Lower to Upper Devonian of the southern border of the Dinant basin, the Upper Devonian of Boulonnais; the Lower Devonian of the Rheinischen Schiefergebirge, and the Middle Devonian of the Eifel. The stratigraphical succession of the Dinant basin is given by Maillieux (1922, 1941), together with stratigraphical correlations with the Rheinischen Schiefergebirge (1922). The succession of the Boulonnais inlier is presented by Pruvost (1924), and that of the Eifel by Struve (1963).

The stratigraphical distribution of the species studied from these regions is shown on text-fig. 1.

*Abbreviations.* In the following descriptions, relevant museum collections listed are as follows: BC—Bedford College, University of London; BM—British Museum (Natural History); GSM—Geological Survey Museum (London); GMUS—Geology Museum, University of Saskatchewan; HMUG—Hunterian Museum, University of Glasgow; IRSN—Institut royal des sciences naturelles de Belgique; MNB—Museum für Naturkunde, Berlin (Haupt-Sammlung); SMF—Senckenberg Museum, Frankfurt.

In each text-fig. of serial sections, the numbers represent distances in millimetres measured anteriorly from the umbones. Muscle field patterns and vascular markings are also illustrated on figures of internal moulds, since moulds, rather than discrete valves, are the common form of preservation.

## SYSTEMATIC DESCRIPTIONS

Suborder DALMANELLOIDEA Moore 1952

Family SCHIZOPHORIIDAE Schuchert and Le Vene 1929

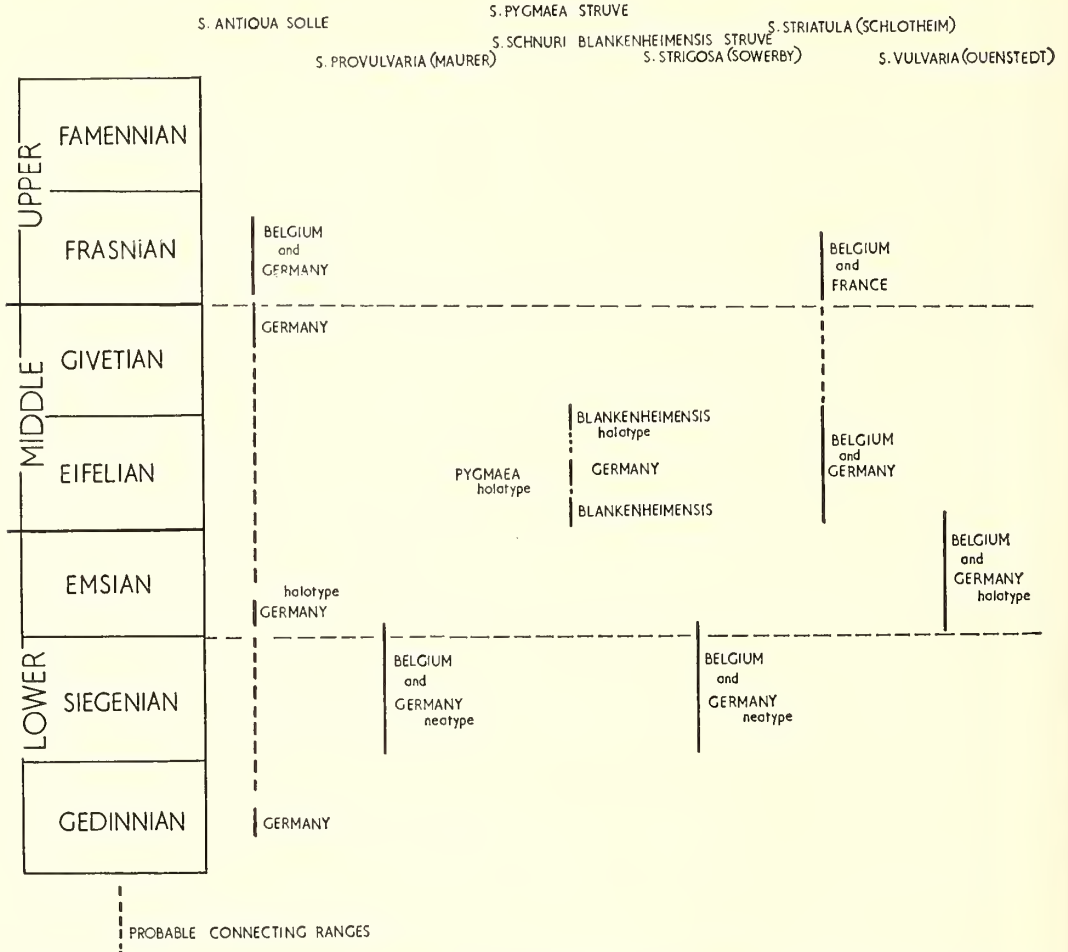
Subfamily SCHIZOPHORIINAE Schuchert and Le Vene 1929

Genus SCHIZOPHORIA King 1850

*Type species.* *Conchylolithus Anomites resupinatus* Martin 1809.

Outline transversely rectangular to elliptical, quadrate to rounded, ventribiconvex to biconvex to dorsibiconvex, the dorsal valve generally deeper in adult forms. Ventral valve convex umbonally, flattening laterally, depressed medially. Dorsal valve evenly convex longitudinally, or greatest convexity umbonally, flattening laterally and anteriorly. Hinge-line straight, submegathyrid; cardinal angles rounded. Beaks small, pointed, incurved; brachial beak more incurved. Interareas curved to beaks, pedicle interarea higher; delthyrium and notothyrium open. Anterior commissure varying from

rectimarginate to uniplicate, unisulcate, sulcificate, biplicate. Dorsibiconvexity and height of anterior plication increase with age. Ventral sulcus frequently developed; dorsal fold occasionally developed adjacent to anterior commissure. Shell costellate, rugate, punctate. Costellae separated by narrower, more angular striae, costellae increasing by bifurcation and intercalation. Growth rugae variably developed with age,



TEXT-FIG. 1. Stratigraphical range of species of *Schizophoria* from Belgium, NE. France, and Germany.

and between species, concentrated anteriorly and laterally. Puncta subrounded, concentrated along striae on shell surface, concentrated along costellae in lower shell layers, evenly distributed in inner shell layers.

Ventral muscle field parallel-sided or flabellate, bounded posteriorly by dental lamellae supporting compound teeth, laterally and anteriorly by ridge-like extensions of lamellae. Ridges decreasing in height anteriorly, reflexed, uniting with end of median septum generally to form anterior re-entrant. Diductor muscle field longitudinally divided by median septum, originating near apex of delthyrial cavity. Adductor muscles attached to

median septum. Two subparallel vascula media originating from anterior of muscle field. Genital markings developed laterally and postero-laterally. Shell partially filling delthyrial cavity, decreasing in thickness and disappearing anteriorly.

Dorsal valve with simple or compound serrated myophore. Compound form consisting of central ridge bounded by two to four shorter, narrower ridges (one or two either side). Myophore bounded by divergent or curved brachiophore plates supporting stubby brachiopores. Shell partially filling notothyrial cavity, decreasing in thickness and disappearing anteriorly. Ventral teeth articulating with dorsal sockets. Sockets oval in transverse section, bounded internally by smaller, shallower accessory sockets, and externally by larger, irregularly shaped accessory cavities. Dorsal muscle field generally one-third to one-half valve length, quadripartite, bounded posteriorly by brachiophores, brachiophore plates, laterally and anteriorly by accessory ridges. Ridges decreasing in height anteriorly, reflexed to form anterior re-entrant, uniting with median septum. Median septum originating at base of notothyrial cavity. Minor septum frequently dividing each half of adductor muscle field into pyriform anterior scar and digitate or tripartite posterior scar. Four subparallel vascula media originating from anterior of muscle field. Two vascula myaria occasionally developed laterally to vascula media from ends of minor septa. Genital markings developed laterally and postero-laterally.

*Schizophoria antiqua* Solle

Plate 66, figs. 1a, b; text-figs. 2-5

1907 *Orthis (Schizophoria) striatula* Schlotheim; Walther, p. 279, pl. 13, fig. 9.

1910 *Orthis striatula* Schlotheim; Assman, p. 161, pl. 9, figs. 1, 2.

1916 *Orthis striatula* Schlotheim; Viétor, p. 452, pl. 18, fig. 10.

1936 *Schizophoria antiqua* Solle, p. 208, figs. 14, 15.

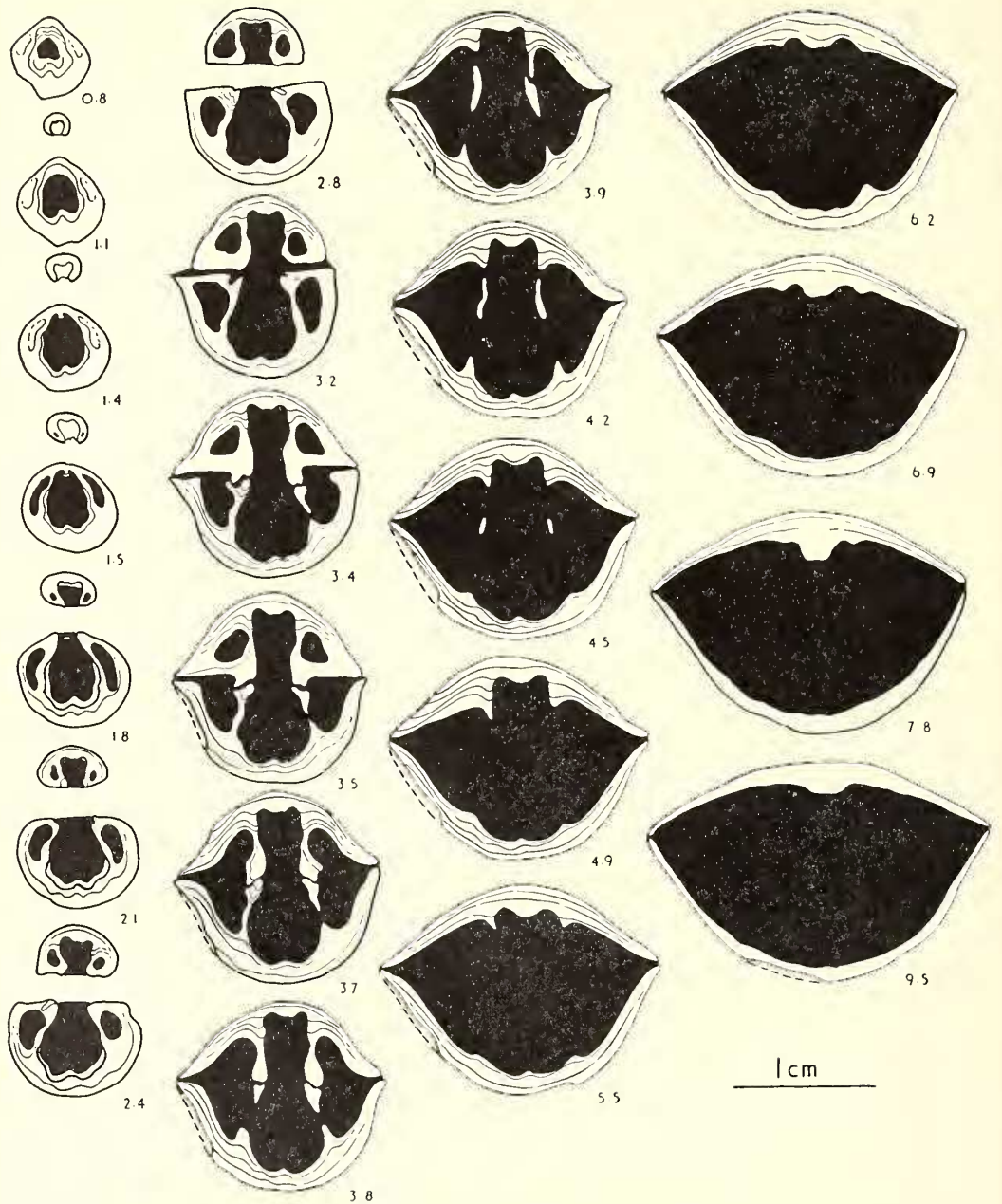
*Type.* The holotype, Nr. XVII 533a, and specimen Nr. XVII 533b are deposited in the Senckenberg Museum, Frankfurt.

*Diagnosis.* Medium to small, rectangular to elliptical, rugate shell, dorsibiconvex in adult form. Ventral muscle field strongly incised, flabellate, with broad, rounded median septum. Dorsal muscle field longitudinally elliptical, bounded posteriorly by curved brachiophore plates.

*Description.* Shell medium to small, ventribiconvex to dorsibiconvex, rectangular to elliptical, with greatest shell width at mid-length. Ventral sulcus ill-defined, originating near anterior border. Low, broad, subrounded anterior uniplication. Costellae coarse, 4 to 5 in 1 mm. at 10 mm. from beaks. Prominent growth rugae.

Teeth compound, supported by anteriorly divergent ventrally subparallel to divergent dental lamellae (text-fig. 2, sections 1.8-3.8). Ventral muscle field (text-fig. 3a) one-third to one-half valve length, flabellate, strongly incised. Deep, broad, rounded anterior re-entrant. Median septum generally prominent, rounded, broadening and increasing in height, and becoming flat-topped anteriorly (text-fig. 2, sections 1.1-9.5). Two slightly divergent vascula media. Genital markings developed postero-laterally (text-fig. 3a).

Myophore small, simple or rudimentarily compound, with central ridge bordered by two lateral ridges. Stubby brachiophores fused to strong, curved brachiophore plates (text-fig. 2, sections 1.4-3.8). Dental sockets oval, articulating with ventral teeth (text-fig. 2, sections 3.4, 3.5). Dorsal muscle field (text-fig. 3b) moderately incised,



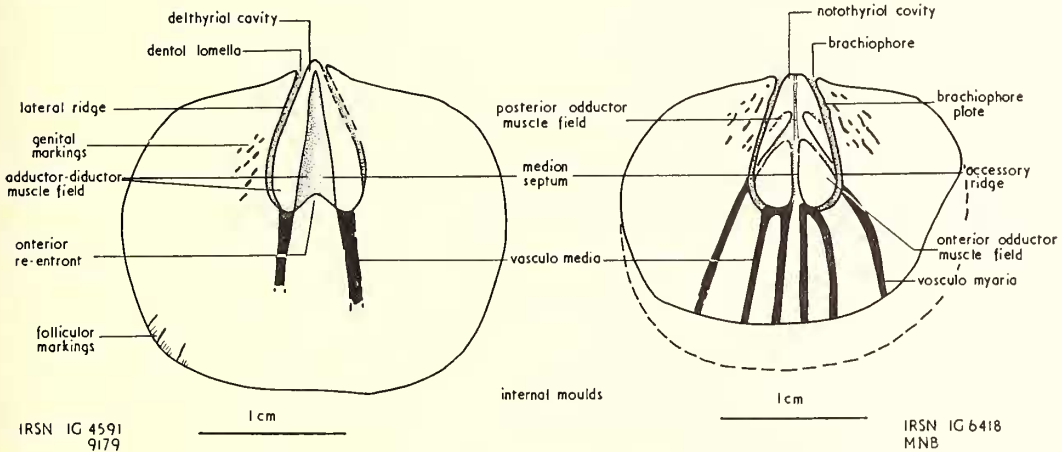
TEXT-FIG. 2. *Schizophoria antiqua* Sollé. Transverse serial sections (IRSN IG6154).

longitudinally elliptical, with greatest width anteriorly, one-third to one-half valve length. Accessory ridges continuous with brachiophore plates, smoothly reflexed anteriorly. Median septum angular, increasing in height and broadening very slightly anteriorly (text-fig. 2, sections 0.8–5.5). Anterior adductor muscle scar pyriform; posterior muscle scar possibly digitate. Four weakly divergent *vascula media*, and pair of divergent *vascula myaria* (text-fig. 3*b*). Genital markings developed postero-laterally.

*Dimensions.* External dimensions and muscle field dimensions are plotted on text-fig. 4.

a VENTRAL MUSCLE FIELD

b DORSAL MUSCLE FIELD



TEXT-FIG. 3. *Schizophoria antiqua* Solle. Ventral and dorsal muscle fields.

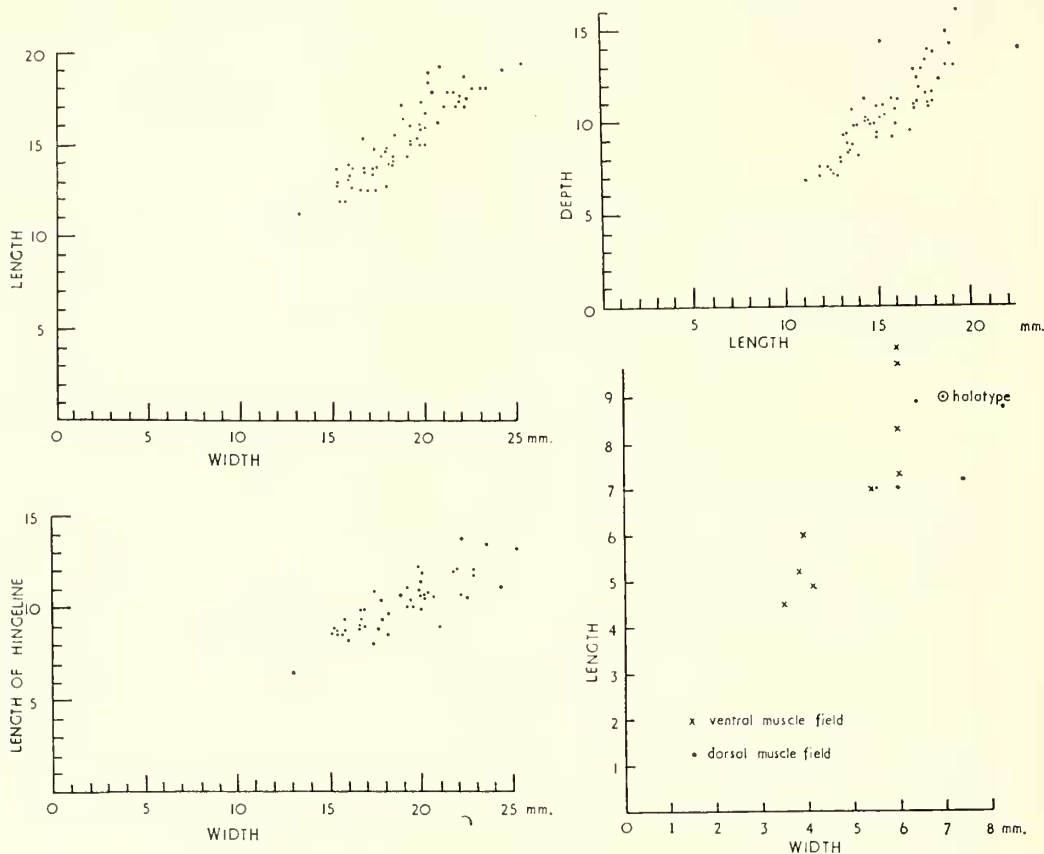
*Remarks.* Although Solle described *Schizophoria antiqua* from the Lower Devonian (Emsian) of Germany, the bulk of the material examined is deposited in the Institut royal des sciences naturelles de Belgique, and was collected from the Frasnian of the Dinant Basin. Two additional specimens from the Museum für Naturkunde, Berlin, collected from the Gedinnian of the Taunus region, extends the range of the species. This medium to small, tumid, rugate form of *Schizophoria* is distinct from other Devonian species (text-fig. 5).

*Schizophoria antiqua* closely resembles *S. woodi* Bond of the Carboniferous in outline, tumidity, prominent growth rugae, curved brachiophore plates, and flabellate pedicle muscle field. There is a closer resemblance in size with the smaller form of *S. woodi* from the Treak Cliff, Cracoe, and Craven areas of reef limestone. But *S. antiqua* is more coarsely costellate, lacks spine bases, and the brachial muscle field is more elliptical in outline.

Youthful forms of *S. antiqua* resemble *S. connivens* (Phillips) of the Carboniferous, in rectangular outline and coarse costellae, but internally there are distinct differences. The flabellate ventral muscle field, and broad median septum, contrast with the less flabellate, elliptical form and narrower septum of *S. connivens*. The elliptical dorsal muscle field, curved brachiophore plates, and six pallial sinus trunks of *S. antiqua* contrast with the elliptical to rounded muscle field, divergent brachiophore plates, and four pallial sinus trunks of *S. connivens*.

*Material.* Belgium: Frasnian, Assise de Frasnes (F2)-F2d (IRSN IG5911, 6154, 8439, 9179), F2h (IRSN IG4591, 6418), F2i (IRSN IG8701), Dinant basin. Germany: Gedinnian, Hobrächer Schichten (MNB), Taunus; Lower Emsian (MNB), Villmar. Middle Devonian (MNB), Boppard; Lower Frasnian (BC B1-9), Paffrather Syncline, near Cologne; Upper Middle Devonian (SMF), Villmar.

S. ANTIQUA SOLLE



TEXT-FIG. 4. Dimensions of *Schizophoria antiqua* Solle.

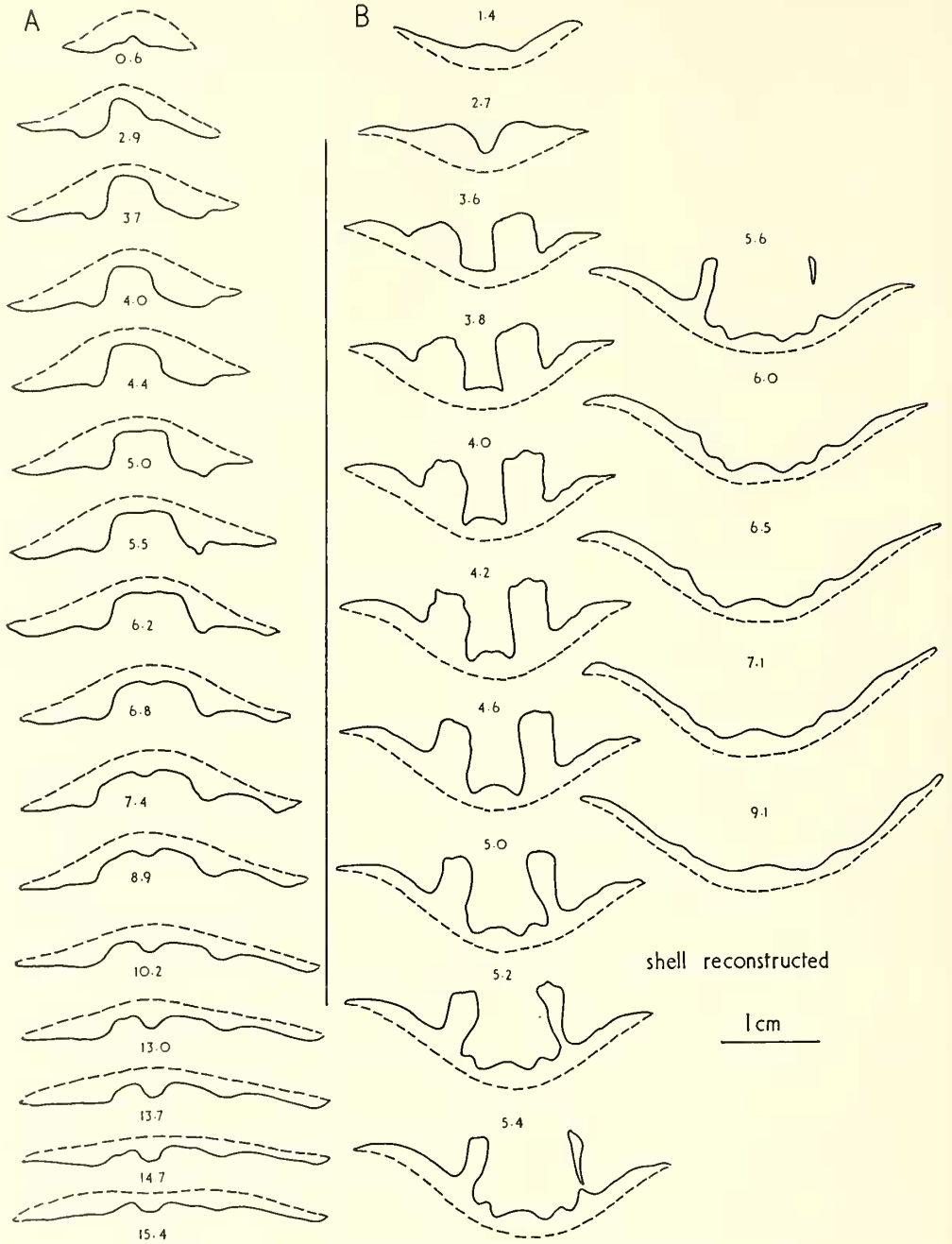
*Schizophoria provulvaria* Maurer

Plate 66, figs. 2, 3, 10; text-figs. 6-9

- 1864-5 *Orthis hipparionix* Vanuxem (?); Davidson, p. 90, pl. 17, figs. 9, 10? *non* 8, 11.  
 1886 *Orthis provulvaria* Maurer, p. 21.  
 1890 *Orthis personata* Zeiler; Kayser, pl. 12, fig. 3.  
 1893 *Orthis provulvaria* Maurer; Maurer, p. 7, pl. 3, figs. 1-4.  
 1904 *Orthis (Schizophoria) provulvaria* Maurer; Drevermann, p. 267, pl. 30, figs. 29? 30; pl. 31, figs. 11-19 (11? 16? 18?).  
 1936 *Schizophoria provulvaria* Maurer; Termier and Termier, p. 1126, pl. 3, figs. 3, 4; 1950, pl. 71, figs. 10, 11?; pl. 72, figs. 12? 13?  
 1938 *Schizophoria provulvaria* (Maurer); Shirley, p. 465, pl. 4, figs. 10-13.  
 1942 *Schizophoria provulvaria* (Maurer); Gill, p. 36, pl. 6, fig. 1.

	SIZE	OUTLINE	CONVEXITY ORNAMENT	DENTAL LAMELLAE	VENTRAL MUSCLE FIELD	BRACHIOPHORES BRACHIOPHORE PLATES	DORSAL MUSCLE FIELD
<u>Schizophoria antiqua</u> Solle	medium small	rectangular elliptical	dorsibiconvex tumid	ventrally subparallel to divergent	broad flabellate strongly incised	stubby brachiophores; curved brachiophore plates	elongate oval, moderately incised
<u>Schizophoria provulvaria</u> (Maurer)	large	elliptical	dorsibiconvex	ventrally subparallel to convergent	broad flabellate strongly incised	stubby brachiophores; strong subparallel brachiophore plates	rectangular elliptical, moderately incised; digitate posterior adductor scars
<u>Schizophoria pygmaea</u> Struve	small	rectangular elliptical	weakly dorsibiconvex generally thin form	ventrally divergent	broad flabellate strongly incised	stubby brachiophores; curved brachiophore plates	rectangular rounded, moderately incised
<u>Schizophoria schnuri</u> blankenheimensis Struve	large	rectangular elliptical	weakly dorsibiconvex generally thin form	ventrally divergent	broad flabellate strongly incised	stubby brachiophores; curved brachiophore plates	rectangular rounded, moderately incised; digitate posterior adductor scars
<u>Schizophoria striatula</u> (Schothheim)	medium large	quadrate elliptical	dorsibiconvex	ventrally subparallel to divergent	elongate oval flabellate strongly incised	stubby brachiophores; strong divergent brachiophore plates	quadrate rounded, moderately incised; digitate posterior adductor scars
<u>Schizophoria strigosa</u> (Sowerby)	medium large	quadrate elliptical	dorsibiconvex	—	broad elongate oval flabellate strongly incised	—	quadrate rounded, moderately incised; digitate posterior adductor scars
<u>Schizophoria vulvaria</u> (Quenstedt)	large	quadrate rectangular elliptical	dorsibiconvex	ventrally convergent	elongate oval flabellate strongly incised	stubby brachiophores; strong divergent brachiophore plates	quadrate rounded, moderately incised; digitate tripartite posterior adductor scars

TEXT-FIG. 5. Comparisons of Devonian species of *Schizophoria*.



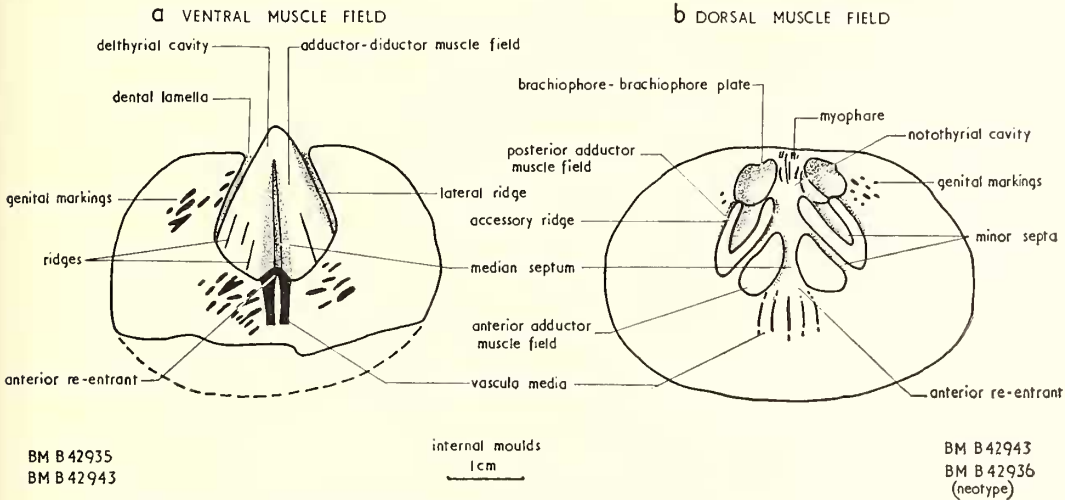
TEXT-FIG. 6. *Schizophoria provulvaria* (Maurer). Transverse serial sections of plaster internal moulds. A—ventral valve (HMUG L5345/2), B—dorsal valve (HMUG L5341/2).



*Type.* Maurer's specimens (1886, 1893) cannot be traced. These were collected from the Lower Devonian of Seifen, Germany. A neotype has been selected, BM B42943, a dorsal internal mould. This was also collected from the Lower Devonian of Seifen, Dierdorf.

*Diagnosis.* Shell large, elliptical. Ventral muscle field broad, flabellate, strongly incised, with broad, rounded median septum. Brachiophores-brachiophore plates thick, sub-subparallel to divergent. Short peripheral follicular markings.

*Description.* Shell mould large, dorsibiconvex, elliptical in outline, with greatest width at or slightly anterior to midlength. Anterior commissure rounded uniplicate.



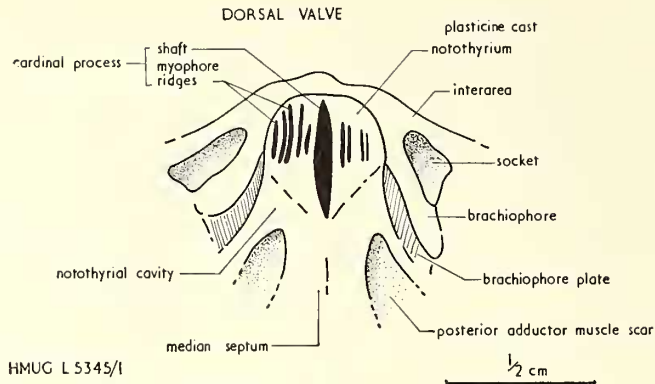
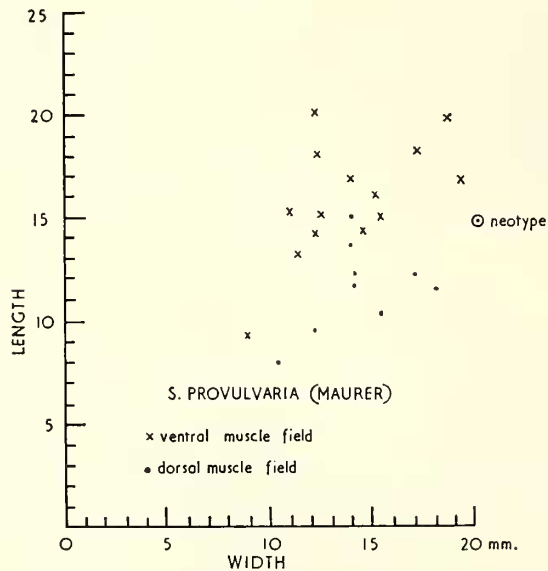
TEXT-FIG. 7. *Schizophoria provulvaria* (Maurer). Ventral and dorsal muscle fields.

Ventral muscle field (text-fig. 7a) one-half to two-thirds valve length, broad, flabellate, strongly incised. Subrounded anterior re-entrant. Median septum narrow, rounded, rapidly broadening and increasing in height anteriorly (text-fig. 6a, sections 6.2–15.4). Two parallel vascula media originating in anterior re-entrant of muscle field. Genital markings developed laterally and postero-laterally (text-fig. 7a).

Prominent cardinal process; broad, compound myophore, narrow shaft (text-fig. 8). Stubby brachiophores fused to strong, thick, subparallel to divergent brachiophore plates (text-fig. 6b, sections 3.6–5.6). Dorsal muscle field (text-fig. 7b) moderately incised, transversely rectangular to elliptical, one-half valve length. Low accessory ridges smoothly reflexed anteriorly to form shallow, sub-rounded anterior re-entrant. Median septum low, broad, rounded, narrowing anteriorly (text-fig. 6b, sections 3.8–7.1). Anterior adductor muscle scar pyriform; posterior muscle scar more incised, digitate, with slightly longer inner lobe (text-fig. 7b). Two vascula media, each bifurcating (text-fig. 7b). Short follicular markings developed peripherally.

*Dimensions.* Dimensions of available muscle fields are plotted on text-fig. 9.

*Remarks.* Apart from a few doubtful specimens assigned to *S. provulvaria* preserved as fragmentary external moulds and illustrating a coarsely costellate shell, all specimens are preserved as fragmentary internal moulds. Serial sections of plaster internal moulds

TEXT-FIG. 8. *Schizophoria provulvaria* (Maurer). Cardinalia.TEXT-FIG. 9. Dimensions of muscle fields of *Schizophoria provulvaria* (Maurer).

## EXPLANATION OF PLATE 66

- Fig. 1. *Schizophoria antiqua* Solle. 1 a, b, Ventral and dorsal views of internal mould, MNB ( $\times 1\frac{1}{2}$ ).  
 Figs. 2, 3, 10. *Schizophoria provulvaria* (Maurer). 2, Internal mould of dorsal valve, neotype, BM B42936 ( $\times 1$ ). 3, 10, Internal moulds of dorsal valves, MNB ( $\times 1$ ).  
 Fig. 4. *Schizophoria pygmaea* Struve. 4 a, b, Dorsal and anterior views, BC B55 ( $\times 2$ ).  
 Fig. 5. *Schizophoria schmuri blankenheimensis*. 5 a-c, Dorsal, ventral, and lateral views, BC B68 ( $\times 1$ ).  
 Figs. 6, 7. *Schizophoria striatula* (Schlotheim). 6, Ventral view, BC B90 ( $\times 1$ ). 7, Lateral view, BC B108 ( $\times 1$ ).  
 Figs. 8, 9, 11, 12. *Schizophoria strigosa* (Sowerby). 8, Internal mould of dorsal valve, neotype, MNB B102.1 ( $\times 1$ ). 9, 11, Internal moulds of dorsal valves, MNB ( $\times 1$ ). 12, Internal mould of dorsal valve, IRSN IG8219 ( $\times 1$ ).  
 Fig. 13. *Schizophoria vulvaria* (Quenstedt). 13 a, b, Ventral and dorsal views of internal mould, BM B62947 ( $\times 1$ ).



1a



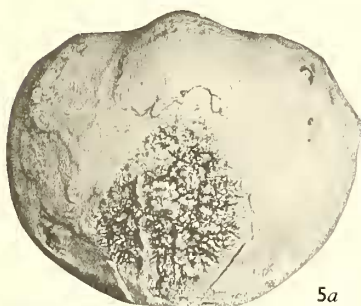
2



3



1b



5a



5b



4a



4b



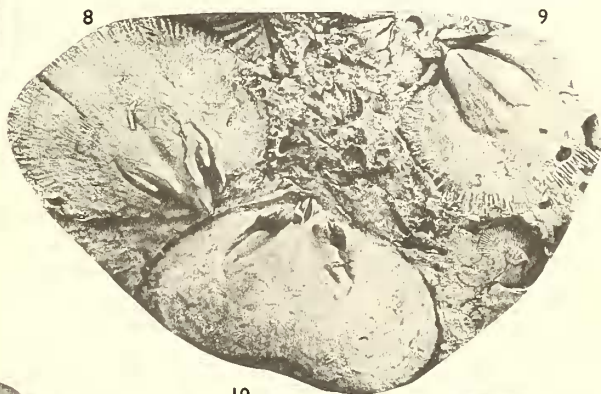
5c



6



7



8

9



13a



13b



10



11



12



(Stanley, 1964) show the general appearance of internal structures. Only discrete valves were available, showing no ventral–dorsal valve relationship (text-fig. 6).

*S. provulvaria* (Maurer) superficially resembles *S. strigosa* (Sowerby). Comparisons are listed under *S. strigosa* (see text-fig. 5). *S. provulvaria* is distinguished externally from *S. vulvaria* (Quenstedt) by its wider outline. Internally, the flabellate ventral muscle field, broad median septum, and deep anterior re-entrant, contrast with the longer, lanceolate to weakly flabellate muscle field, narrow septum, and shallow, or lack of re-entrant of *S. vulvaria*. The moderately incised, rectangular dorsal muscle field, thick brachiophores and parallel-to-divergent brachiophore plates, and bipartite posterior adductor muscle scars of *S. provulvaria* contrast with the more quadrate, strongly incised muscle field, thinner brachiophores and divergent brachiophore plates, and commonly tripartite posterior muscle scar of *S. vulvaria*.

Davidson's use of *Orthis hipparionyx* (1864–5 p. 90) for his specimens resembling *S. provulvaria* is invalid. He did state that his large internal moulds resembled *Orthis hipparionyx* of American authors, but could not be certain as to their identification. The genus *Hipparionyx* was established by Vanuxem in 1842, and is synonymous with the genus *Streptorhynchus* King. In 1853, Schnur, working in the Eifel, discovered specimens with a similar flabellate ventral muscle field, which he considered belonged to the genus *Orthis*, and changed Vanuxem's nomenclature to *Orthis hipparionyx*. But Schnur's specimens are orthotetid brachiopods. Davidson (1864–5) presumably recognized the flabellate ventral muscle field of his specimens and listed them in synonymy with Schnur's *Orthis hipparionyx*.

*Material.* Belgium, Dinant Basin: Siegenien, Grès d'Anor, Sg 2 (IRSN IG12533); Grauwacke de Saint-Michel, Sg 3 (IRSN IG5382, 5746, 8219); Grauwacke Inférieur de Laroche, Sg 3III (IRSN IG9382). Quartzophyllades de Saint-Vith, Sg 5III (IRSN IG8633); Emsien Inférieur, Grauwacke de Pesche, Em 1a (IRSN IG8791); Grès de Mormont, Em 1g (IRSN IG8390). Germany: Lower Devonian (BM B24563, B24565, B42935, 6, B42942, 3, B42945, 6, B49,920, HMUG L5341/4), Seifen, Dierdorf. Siegener Schichten (HMUG L5345/1, 2, SMF), Seifen. Siegener Schichten, Rauhflaserschichten (MNB), Seifen. South-west England: Lower Devonian (GSM 49692), New Drive above Hope's Nose, Torquay.

### *Schizophoria pygmaea* Struve

Plate 66, figs. 4a, b; text-figs. 10, 12, 15

1963a *Schizophoria pygmaea* Struve, p. 251, pl. 39, 40.

(See Struve for synonymy.)

### *Schizophoria schmuri blankenheimensis* Struve 1965

Plate 66, figs. 5a–c; text-figs. 11, 13–15

1853 *Orthis striatula* d'Orbigny; Schnur, pl. 38, fig. 1 e–g?

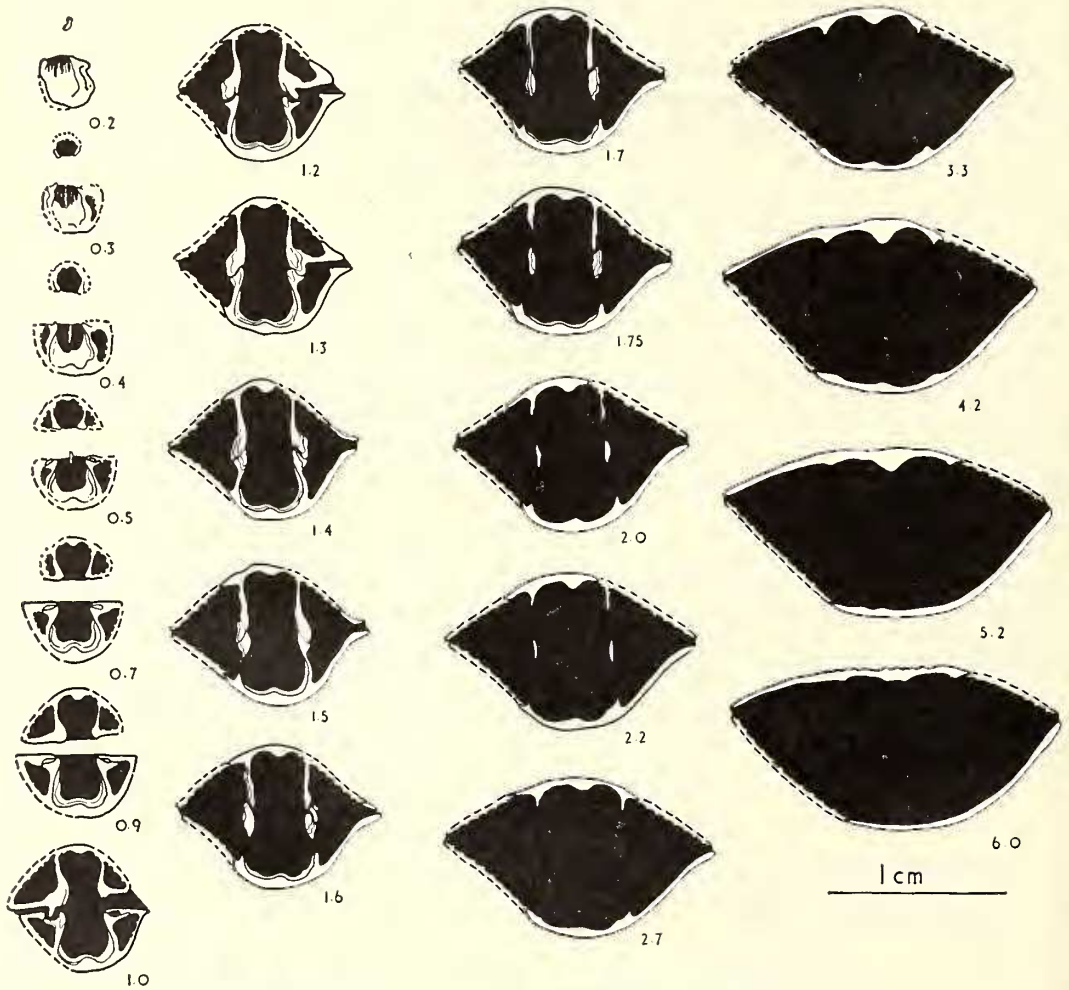
1942 *Schizophoria excisa* (Quenstedt); Spriesterbach, p. 182, pl. 5, figs. 9–14.

*Types.* Struve (1963a) deposited the holotype, SMF 17298, and paratypes of *Schizophoria pygmaea* in the Senckenberg Museum, Frankfurt. The holotype of *Schizophoria schmuri blankenheimensis*, SMF 19559, and paratypes, are also deposited in the Senckenberg Museum.

*Diagnosis.* Shell small (*S. pygmaea*) to large (*S. schmuri blankenheimensis*) rectangular to elliptical, weakly dorsibiconvex, with prominent ventral sulcus. Ventral muscle field

flabellate, strongly incised, with broad, rounded median septum. Strong, curved brachiophore plates.

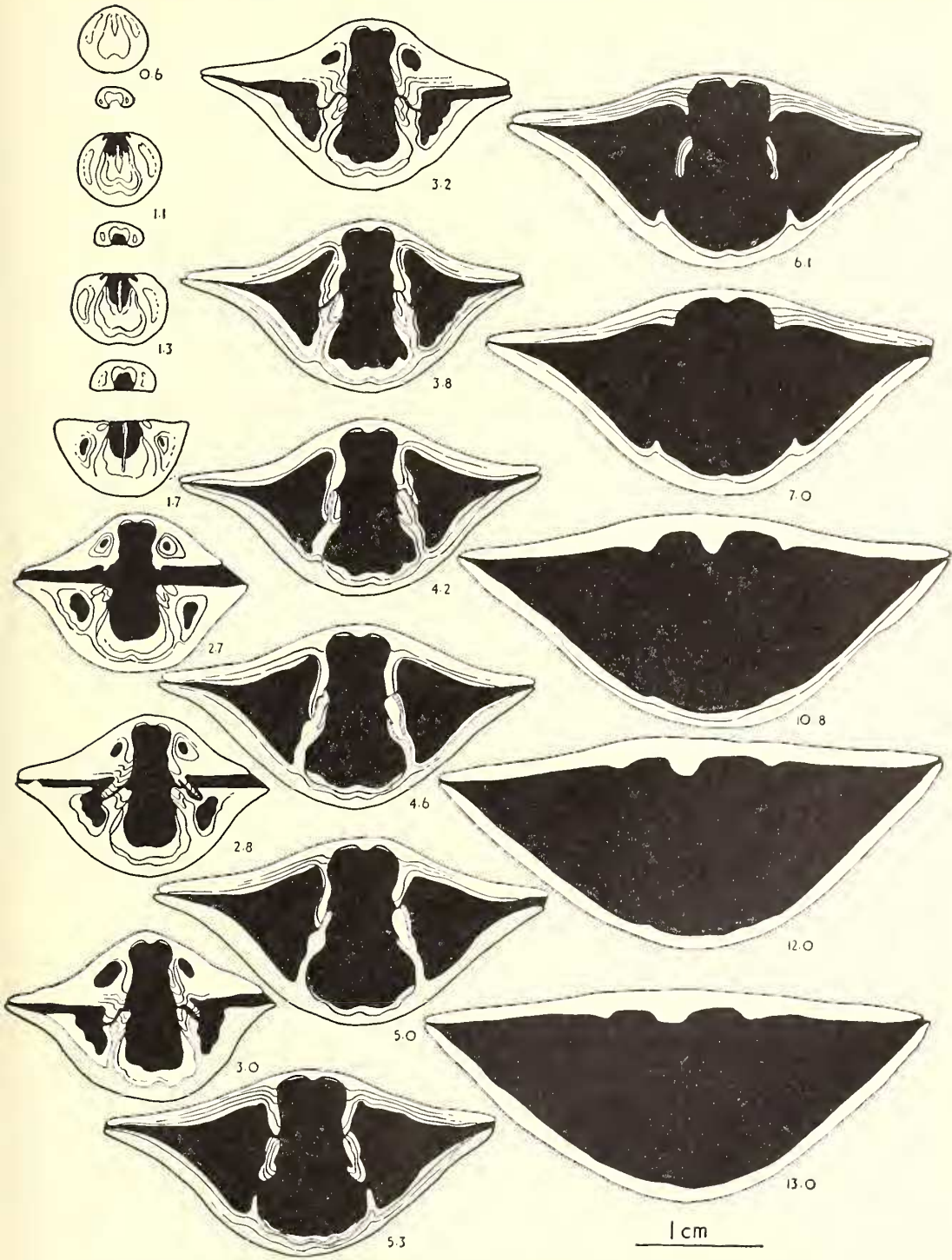
*Description.* Shell small to large, weakly dorsibiconvex, thin, rectangular to elliptical, with greatest width at or anterior to mid-length. Ventral sulcus well defined, originating



TEXT-FIG. 10. *Schizophoria pygmaea* Struve. Transverse serial sections (BC B58).

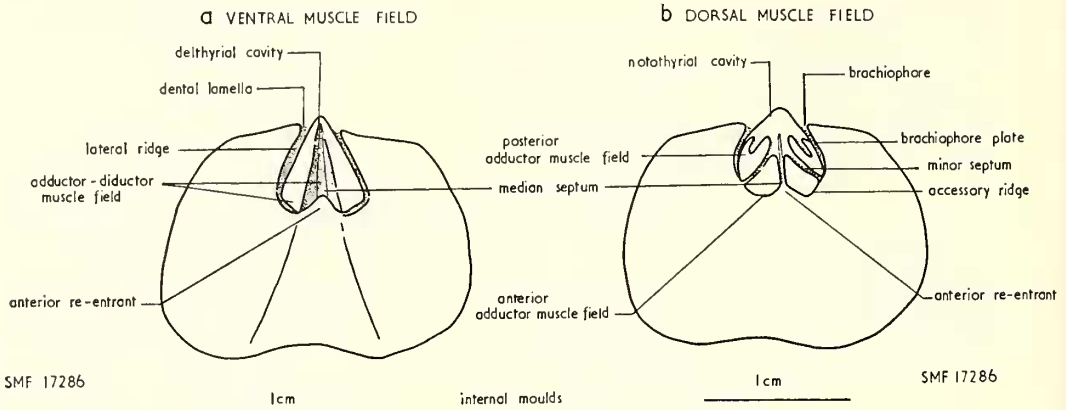
below umbo, flaring and deepening anteriorly. Gentle dorsal fold developed in older specimens. Anterior commissure rounded uniplicate. Costellae fine, 5 to 6 in 1 mm. at 10 mm. from beaks. Spine bases developed at anterior ends of scattered costellae. Growth rugae developed on older specimens.

Teeth prominent, compound, supported by anteriorly and ventrally divergent dental lamellae (text-figs. 10, sections 0.4-1.75; 11, sections 2.2-5.0). Articulation supplemented by interlocking ends of brachiophores and dental lamellae (text-fig. 10, sections

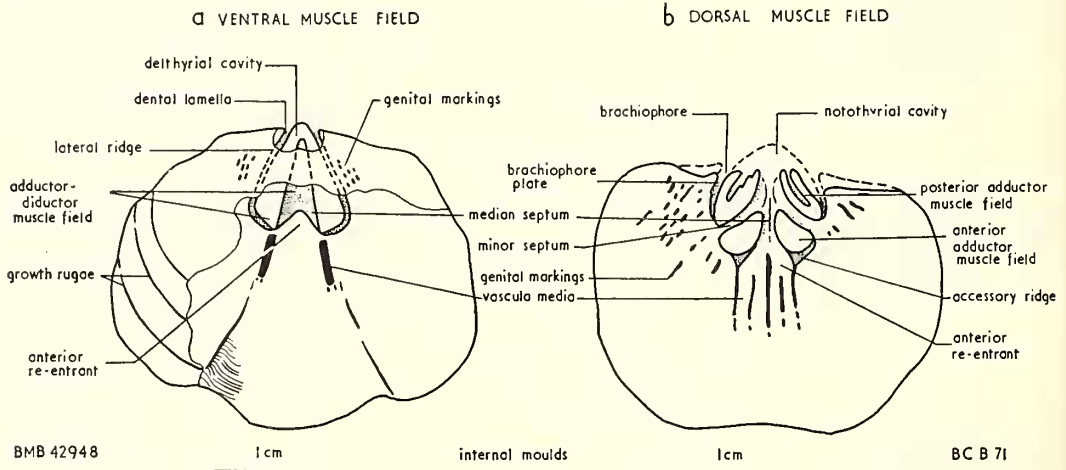


TEXT-FIG. 11. *Schizophoria schuuri blankenheimensis*. Transverse serial sections (BC B70).

1.4-1.6). Ventral muscle field (text-figs. 12, 13) one-third to one-half valve length, flabellate, strongly incised. Deep, subrounded anterior re-entrant. Median septum rounded, broadening and increasing in height, and becoming flat-topped anteriorly (text-figs. 10, sections 0.4-6.0; 11, sections 1.1-13.0). Two *vascula media*; genital markings developed postero-laterally (text-fig. 13).



TEXT-FIG. 12. *Schizophoria pygmaea* Struve. Ventral and dorsal muscle fields.

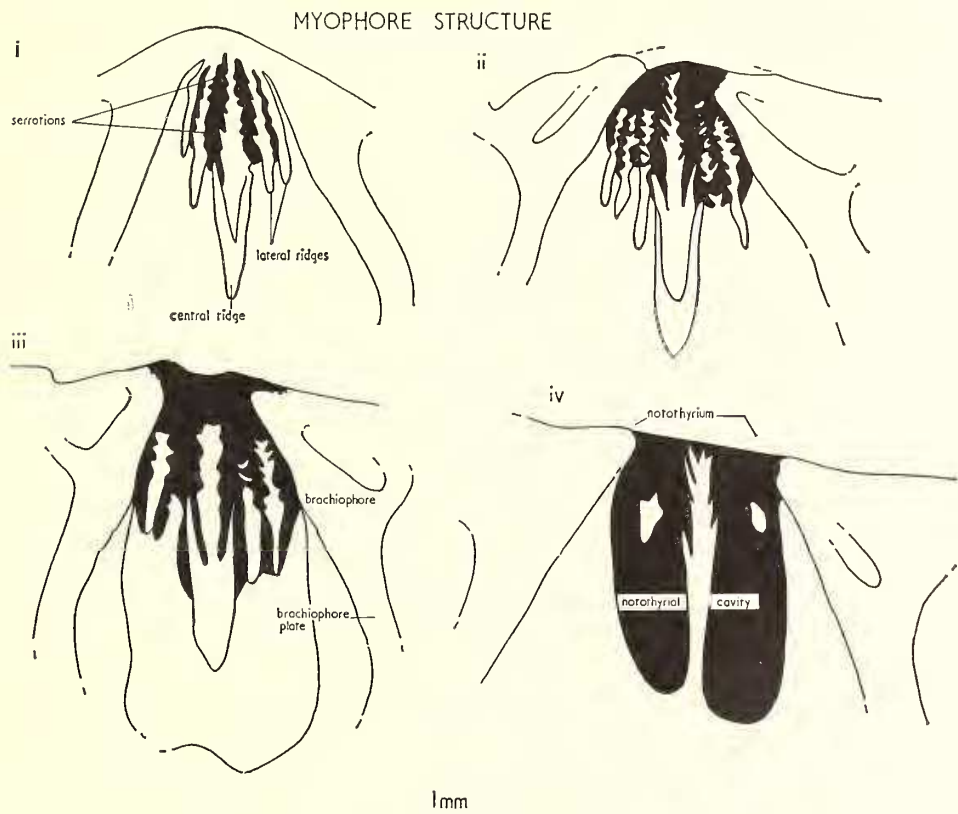


TEXT-FIG. 13. *Schizophoria schuri blankenheimensis*. Ventral and dorsal muscle fields.

Myophore prominent, compound, average width 2.3 mm., with central ridge bordered by four lateral ridges, all finely serrated (text-fig. 14). Stubby brachiophores fused to strong curved brachiophore plates (text-figs. 10, sections 0.4-1.5; 11, sections 1.1-5.3). Brachiophore plates thickened posteriorly by shell filling notothyrial cavity (text-figs. 10, sections 0.5-1.5; 11, sections 2.2-4.2). Deep, oval dental sockets articulating with ventral teeth (text-figs. 10, sections 1.0-1.3; 11, sections 2.8-3.8). Dorsal muscle field (text-figs. 12, 13) moderately incised, rectangular to rounded. Accessory ridges smoothly reflexed anteriorly to form deep subrounded re-entrant. Median septum rounded,



decreasing in width and becoming sharp-crested anteriorly (text-figs. 10, sections 0.4–5.2; 11, sections 1.1–7.0). Anterior adductor muscle scar pyriform, posterior muscle scar digitate, both parts of similar length (text-figs. 12, 13). Two parallel *vascula media*, both bifurcating. Genital markings developed laterally and postero-laterally (text-fig. 13).

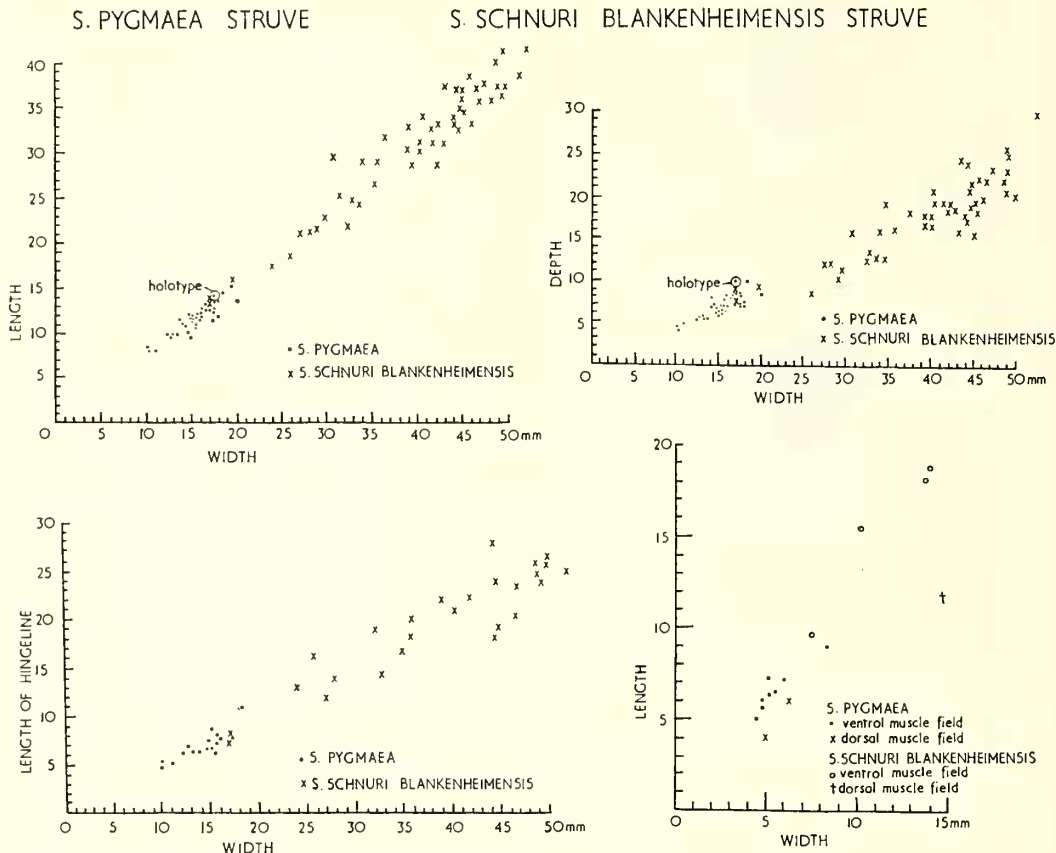


TEXT-FIG. 14. *Schizophoria schmuri blankenheimensis*. Myophore structure.

*Dimensions.* External dimensions and dimensions of muscle fields are plotted on text-fig. 15.

*Remarks.* Struve (1963a, p. 251) described and illustrated a small, relatively thin form of *Schizophoria*, *S. pygmaea*, from the Eifelian Hundsdell, Bildstock, and Flesten Horizons of the Eifel region. Spriesterbach (1942, p. 182) previously described and illustrated a large, relatively thin form of *Schizophoria* from the Middle Devonian of the Blankenheim region, also in the Eifel, which he listed in synonymy with *S. excisa* (Quenstedt). But *S. excisa* (Quenstedt), (Quenstedt 1868–71, p. 561, pl. 55, figs. 138–46) is a separate, distinct form and is synonymous with another species, *S. striatula* (Schlotheim 1813, p. 8, pl. 1, fig. 6; 1820, p. 254, pl. 5, fig. 4). Struve recognized the similarity between *S. pygmaea* and the specimens illustrated by Spriesterbach (1942 pl. 5, figs. 9–14), since he listed the specimen of figure 14 in synonymy with his species. But he made no reference at that time to the larger specimens illustrated on this plate. Figure 14 is probably a more youthful, smaller specimen of the form illustrated by Spriesterbach.

Struve (1965 p. 204) has since described these large specimens under a new subspecies, *S. schnuri blankenheimensis*. His new species, *S. schnuri*, is here considered to be a large form of *S. striatula*, and *S. schnuri blankenheimensis* is considered to be closely related to *S. pygmaea* Struve. *S. pygmaea* appears to be a dwarf form of *S. schnuri blankenheimensis*. Size is the only distinction. The largest (adult) specimens of *S. pygmaea* are



TEXT-FIG. 15. Dimensions of *Schizophoria pygmaea* Struve, and *S. schnuri blankenheimensis*.

comparable with some of the smallest (youthful) specimens of *S. schnuri blankenheimensis* (text-fig. 15). The two forms are similar externally and internally (cf. text-figs. 10, 11 and 12, 13).

The dwarf species, *S. pygmaea*, occurs in the Hundsdell, Bildstock, and Flesten Horizons, where other brachiopods are smaller than normal. This dwarf form is preceded and succeeded stratigraphically by the larger form of *S. schnuri blankenheimensis*. Struve (1965) makes no reference to the similarity between *S. pygmaea* and *S. schnuri blankenheimensis*.

*Schizophoria schnuri blankenheimensis* superficially resembles *S. provulvaria* (Maurer) in the flabellate ventral muscle field and strong median septum, and the dorsal muscle field and four parallel vascula media. However, externally, *S. schnuri blankenheimensis* is

generally less convex, and has a well-defined ventral sulcus. Specimen BC B64, from the lowermost Middle Devonian (Wolfenbach Horizon) is more convex, but when sectioned, illustrated the characteristic internal structures of *S. schuuri blankenheimensis*. *S. pygmaea* resembles *S. provulvaria* in the same manner, but is much smaller in size.

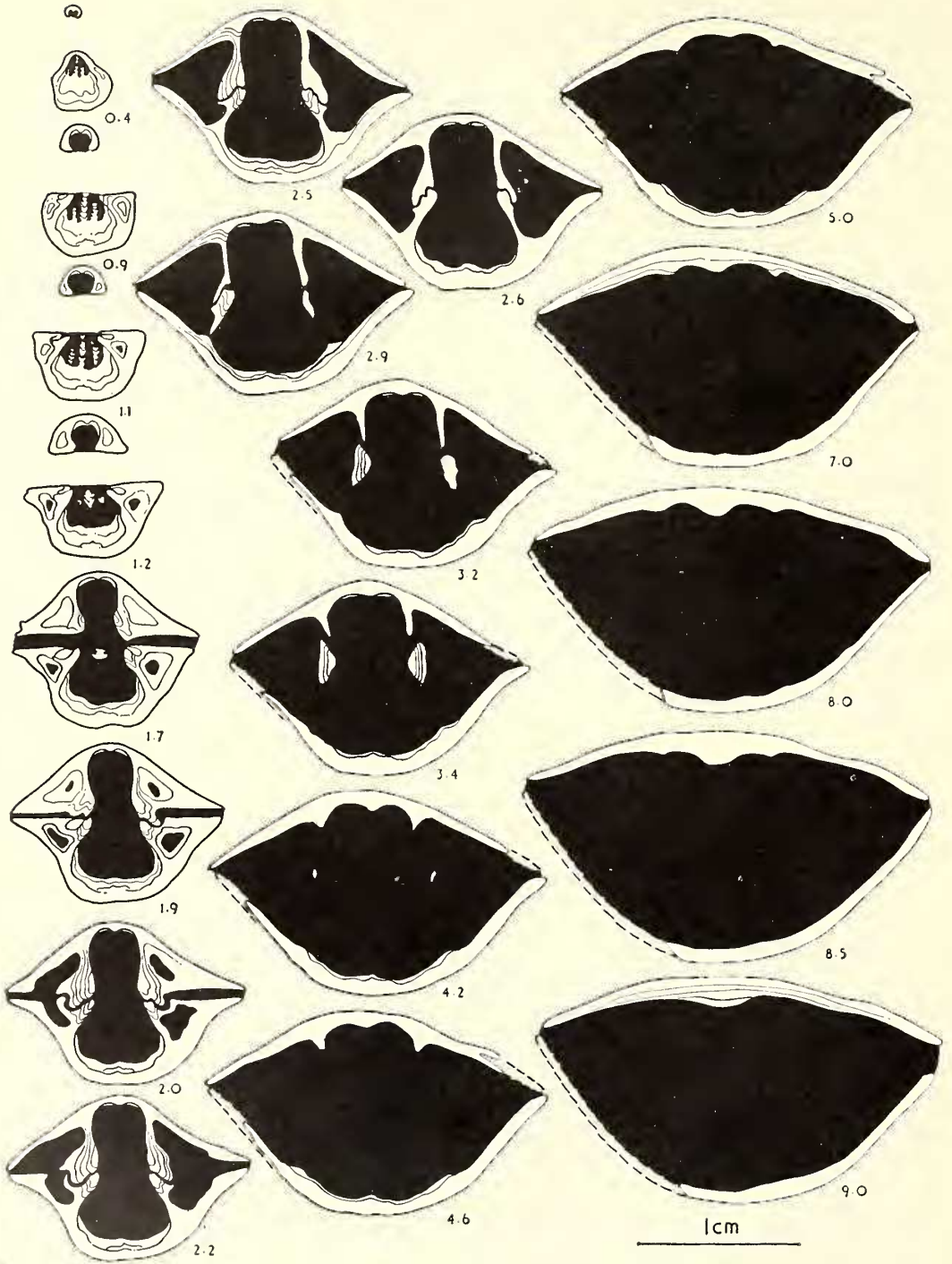
*Schizophoria schuuri blankenheimensis* is distinguished from *S. striatula* (Schlotheim) by its more rectangular outline and weaker convexity. *Schizophoria striatula* is generally more quadrate to rounded, with greatest shell width situated anteriorly. Internally there are muscle field differences (text-figs. 13, 17). The strongly flabellate ventral muscle field, deep re-entrant, broad median septum, and widely separated, slightly divergent vascula media of *S. schuuri blankenheimensis* contrast with the less flabellate to elongate elliptical muscle field, narrower re-entrant and median septum, and closely spaced, parallel vascula media of *S. striatula* from the Middle Devonian. In the dorsal valve, *S. striatula* has a longer inner portion to the posterior adductor muscle scar, divergent pallial sinus trunks, and shorter genital markings. The divergent brachiophore plates also contrast with the curved plates of *S. schuuri blankenheimensis*.

*Material.* Germany, Eifel region: Eifelian, *S. pygmaea*—Ahrdorf Beds, Bildstock Horizon, MTB Dollendorf (BC B10). Same stratigraphical level, MTB Dollendorf (BC B11). Ahrdorf Beds, Flesten Horizon, MTB Dollendorf (BC B12, 13). Same stratigraphical level, MTB Dollendorf (BC B14, 15). Same stratigraphical level, Ahrdorf Syncline, MTB Dollendorf (BC B16–59). Ahrdorf Beds, MTB Mechernich (BC B60–63). Nohn–Ahrdorf Beds, Hundsdell–Bildstock Horizon, Sötenicher Syncline, MTB Mechernich (SMF 17267). Schwirzheim Horizon, Gerolstein (SMF 17278). Ahrdorf Beds, Bildstock Horizon, Hillesheimer Syncline, MTB Dollendorf (SMF 17286). *S. schuuri blankenheimensis*—Lauch Beds, Wolfenbach Horizon, MTB Dollendorf (BC B64). Junkerberg Beds, Blankenheim Railway Cutting (BC B65–67, 69–71). Same stratigraphical level, MTB Blankenheim (BC B72–82). Middle Devonian, Gerolstein (BM B42948). Upper Junkerberg Beds, Blankenheim Railway Cutting (GMUS Eu DE 77(5)). Lower and Upper Middle Devonian, Blankenheim (MNB). Middle Devonian, Gerolstein (MNB).

### *Schizophoria striatula* (Schlotheim)

Plate 66, figs. 6–7; text-figs. 16–20

- 1777 *Terebratulæ minutissime striatae*; Schröter, p. 390, pl. 4, fig. 24.  
 1813 *Anomia terebratulites striatulus* Schlotheim; Leonhard, p. 8, pl. 1, fig. 6.  
 1820 *Terebratulites striatulus*; Schlotheim, p. 254, pl. 15, fig. 4.  
 1841 *Orthis resupinata*; Phillips, pl. 27, fig. 115.  
 1842–4 *Orthis striatula*; De Koninck, p. 224, pl. 13<sup>2</sup>, fig. 6; *non*. pl. 13, fig. 11.  
 1850–6 *Orthis striatula*; Sandberger and Sandberger, p. 355, pl. 34, fig. 4.  
 1851–5 *Orthis striatula*, Schlotheim; Davidson, pl. 7, figs. 128–33.  
 1853 *Spirifer striatulus* Schlotheim sp.; Geinitz, p. 61, pl. 15, figs. 10–12.  
 1853 *Orthis striatula* d'Orbigny; Schnur, p. 215, pl. 38, fig. 1 a–d, h–i; e–g?  
 1860 *Orthis striatula* Schlotheim; Grünewaldt, p. 87, pl. 2, fig. 6.  
 1864–5 *Orthis striatula* Schlotheim; Davidson, p. 87, pl. 17, figs. 4–7.  
 1868–71 *Orthis excisa*; Quenstedt, p. 561, pl. 55, figs. 138–45.  
 1908 *Orthis (Sch) striatula* (Schlotheim); Cowper-Reed, p. 79, pl. 13, figs. 19–24.  
 1922 *Orthis (Schl) striatula* (Schlotheim); Cowper-Reed, p. 34, pl. 6, figs. 12, 13.  
 1930 *Orthis (Schizophoria) resupinata* var. *striatula* (Schloth.); Paeckelmann, p. 158, pl. 9, figs. 3–10.  
 1959 *Schizophoria striatula* (Schlotheim); Biernat, p. 54, pls. 7–9; pl. 10, fig. 3.  
*non* 1907 *Orthis (Schizophoria) striatula* Schlotheim; Walther, p. 279, pl. 13, fig. 9.  
*non* 1916 *Orthis striatula* Schl.; Viétor, p. 452, pl. 18, fig. 10.  
*non* 1932 *Schizophoria* aff. *striatula* (Schlotheim); Schuchert and Cooper, pl. 23, figs. 22–25.

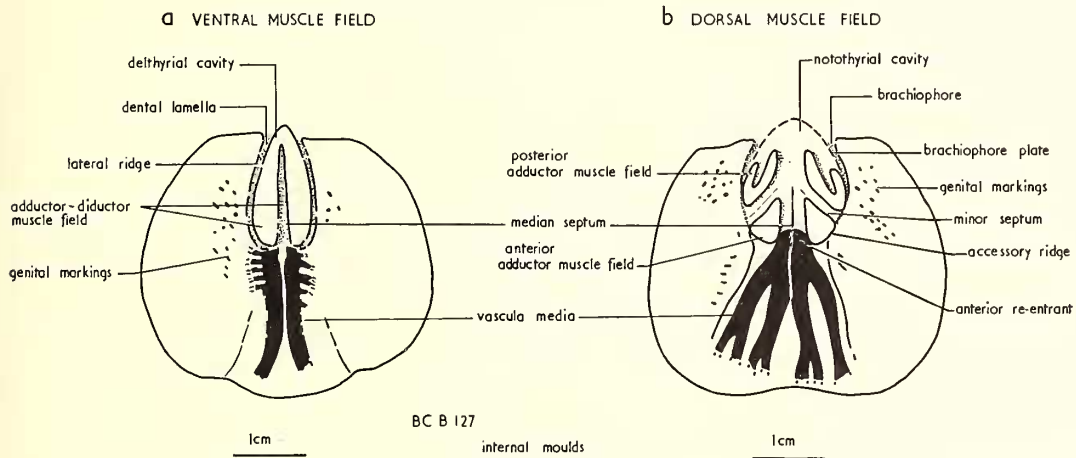


TEXT-FIG. 16. *Schizophoria striatula* (Schlotheim). Transverse serial sections (BC B94).

*Type.* Schlotheim's holotype is deposited in the Museum für Naturkunde, Berlin.

*Diagnosis.* Shell medium to large, elliptical to quadrate, with prominent anterior dorsal fold in older specimens. Ventral muscle field oval to flabellate. Strong divergent brachio-phore plates.

*Description.* Shell medium to large, dorsibiconvex, quadrate to elliptical, with greatest shell width generally anterior to mid-length. Ventral sulcus originating half way along valve, broadening and deepening anteriorly. Dorsal fold developed in older specimens. Anterior commissure rounded uniplicate. Costellae moderately coarse, 4 to 5 in 1 mm. at 10 mm. from beaks. Growth rugae prominent on older specimens.



TEXT-FIG. 17. *Schizophoria striatula* (Schlotheim). Ventral and dorsal muscle fields.

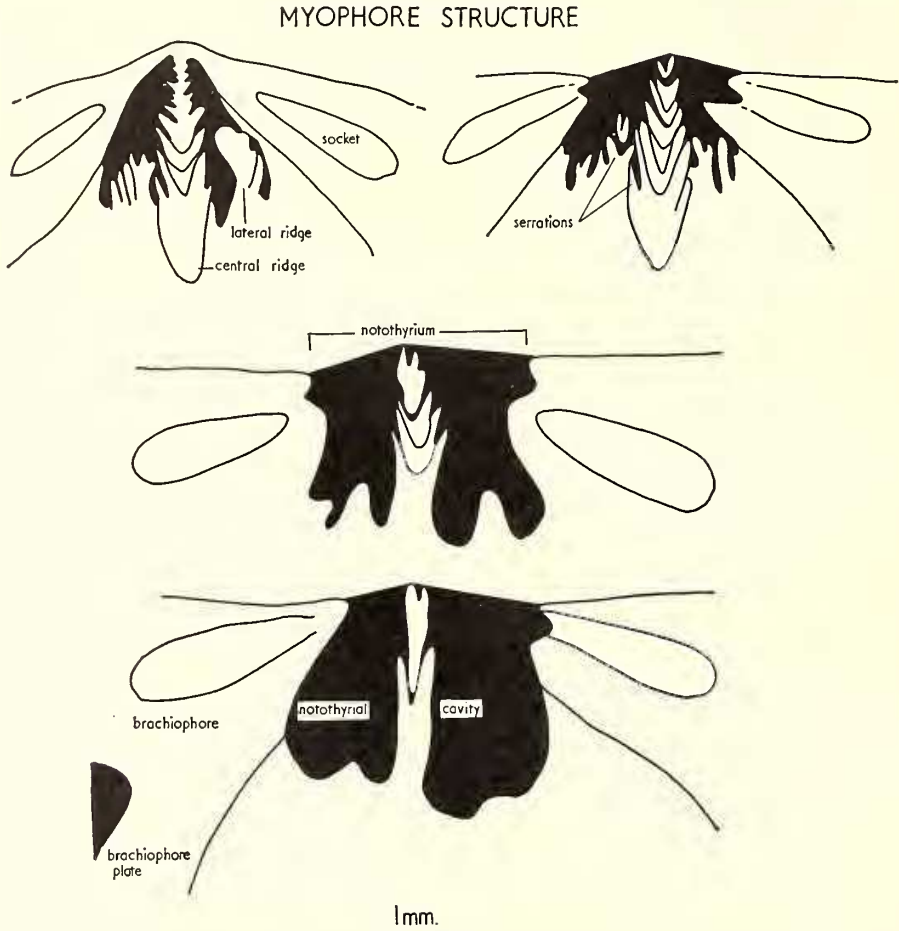
Teeth prominent, compound, supported by anteriorly divergent, ventrally parallel to divergent dental lamellae (text-fig. 16, sections 1.7–3.2). Articulation supplemented by interlocking ends of brachiophores and dental lamellae. Shell partially filling delthyrial cavity (text-fig. 16, sections 0.9–3.4). Ventral muscle field (text-fig. 17a) one-third to one-half valve length, elliptical to flabellate, strongly incised. Rounded anterior re-entrant, or re-entrant absent. Median septum rounded, broadening and increasing in height anteriorly (text-fig. 16, sections 0.4–9.0). Two parallel vascula media, divergent anteriorly. Genital markings developed postero-laterally (text-fig. 17a).

Myophore prominent, compound, average width 3 mm., with central ridge generally bordered by two lateral ridges, all coarsely serrated (text-fig. 18). Stubby brachiophores fused to strong divergent brachiophore plates (text-fig. 16, sections 1.1–3.4). Deep dental sockets articulating with ventral teeth (text-fig. 16, sections 1.9–2.2). Dorsal muscle field incised, quadrate to rounded, one-third to one-half valve length. Accessory ridges smoothly reflexed anteriorly to form moderately deep, rounded re-entrant. Median septum angular to subrounded, broadening and increasing in height, then narrowing anteriorly (text-fig. 16, sections 0.9–7.0). Anterior adductor muscle scar pyriform, with acute apex; posterior muscle scar digitate, with longer inner lobe (text-fig. 17b). Two divergent vascula media, each bifurcating. Two narrower vascula myaria with lateral

markings apparently developed, one either side main trunks. Genital markings developed postero-laterally (text-fig. 17b).

*Dimensions.* External dimensions and dimensions of muscle fields are plotted on text-fig. 19.

*Remarks.* Variation in the form of the ventral muscle field is shown on text-fig. 20.

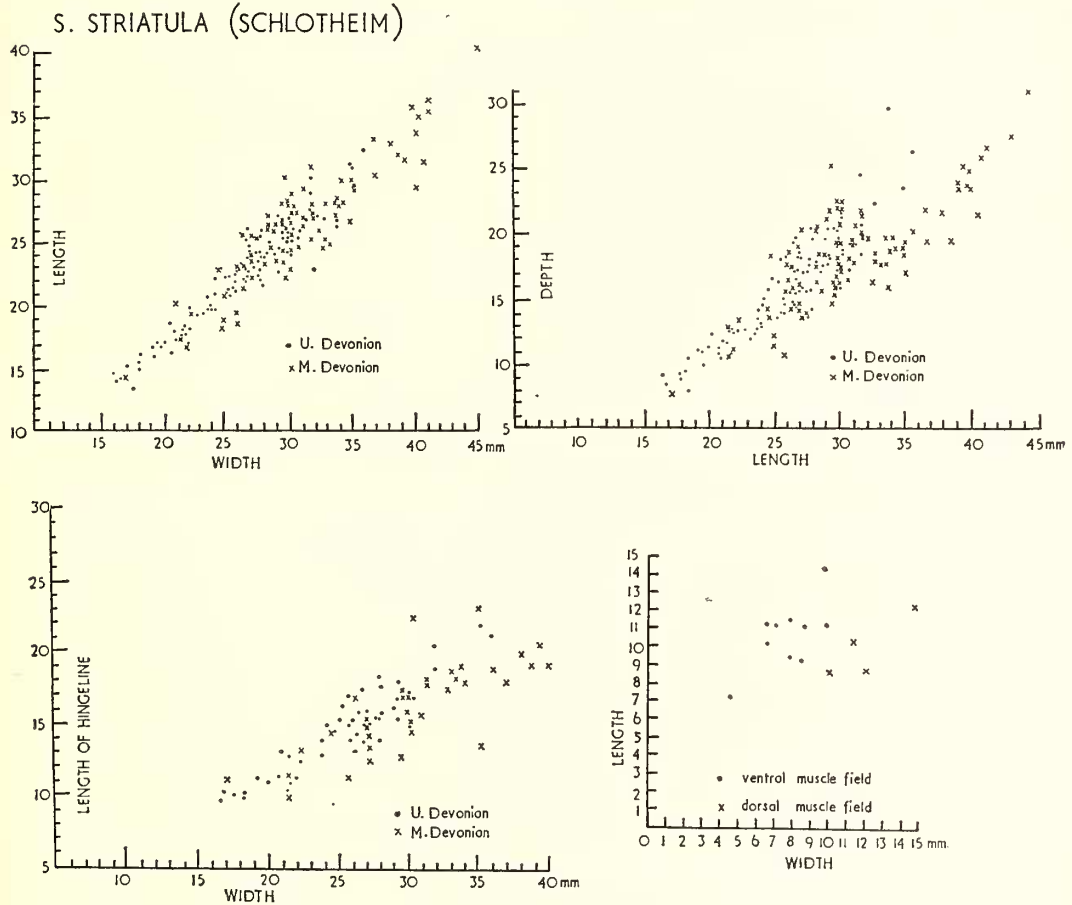


TEXT-FIG. 18. *Schizophoria striatula* (Schlotheim). Myophore structure.

*Schizophoria striatula* (Schlotheim) is a long-ranging species (Eifelian–Frasnian), and shows little variation in morphology, except in size. Although specimens from the Middle and Upper Devonian have been differentiated on text-fig. 19, they have comparable dimensions. But many Upper Devonian specimens lack the characteristic dorsal anterior fold of the Middle Devonian forms, and have their greatest shell width at the mid-length. Internally, the ventral muscle field of many Upper Devonian specimens is more flabellate, with a broader septum. However, specimen BC B131 collected from the Middle Devonian, although representing a minority, has a flabellate muscle field, and

specimen GSM 34/20, an Upper Devonian form, is an exception, with an elliptical muscle field (text-fig. 20).

Specimens of *Schizophoria striatula* from the Geisdorf Horizon (Eifelian) of the Eifel region are much larger. Other members of fauna at this level are also larger. Struve (1965,



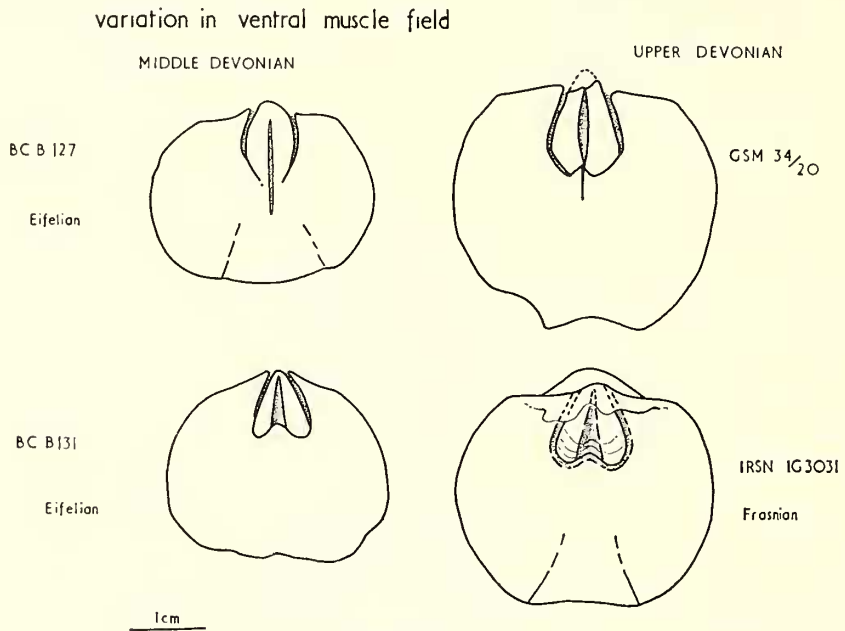
TEXT-FIG. 19. Dimensions of *Schizophoria striatula* (Schlotheim).

p. 202) described a new species, *Schizophoria schnuri*, from the Middle Devonian of the Eifel, which also appears to be a large form of *S. striatula*. At the same time, he established the subspecies *S. schnuri schnuri*, *subexcisa*, *junkerbergiana*, and *biscissa*. There are no illustrations of internal structures, and externally the subspecies could represent variation within *S. striatula*.

*Schizophoria striatula* superficially resembles *S. resupinata* (Martin) of the Carboniferous in general outline and muscle fields. Early workers frequently considered them as one species. But *S. striatula* is generally smaller, more quadrate, lacks a dorsal sulcus, has a higher anterior plication, and lacks spine bases. *Schizophoria resupinata* is frequently larger, rectangular to elliptical, with a rectimarginate to uniplicate to unisulcate

to sulcificate anterior commissure, and is frequently covered in spine bases. The elliptical to weakly flabellate ventral muscle field of *S. striatula* superficially resembles that of *S. resupinata*, and the dorsal muscle fields are comparable.

*Material.* France, Boulonnais: Lower Frasnian, NE. end Carrière Parisienne (BC B83–89); Devonian, Ferques (BM B19213, B82765, B82778); Devonian (BM B26,209). Belgium, Dinant Basin: Couvinien Supérieur (CO 2)—CO 2a (IRSN IG4916, 6887, 8663), CO 2c (IRSN IG4761, 4916, 5127, 9694); Frasnien Moyen (F2)—F2a (IRSN IG3031, 5911, 8254, 11.349), F2b (IRSN IG3349), F2e (IRSN IG4591), F2i (IRSN IG3031, 2731, 4761, 5408). Germany, Eifel region: Eifelian–Lower Nohn beds, Weilersbach Horizon, Hillesheimer Syncline, MTB Dollendorf (BC B90–92); Lower Nohn Beds, low Schleit



TEXT-FIG. 20. *Schizophoria striatula* (Schlotheim). Variation in ventral muscle field.

Horizon, MTB Dollendorf (BC B93, 94); Upper Junkerberg Beds, Geisdorf Horizon, MTB Gerolstein (BC B95); same stratigraphical level, Prüm Syncline (BC B96–98); same stratigraphical level, MTB Mechernich (BC B99). Upper Junkerberg Beds to Upper Freilingen Beds, MTB Gerolstein (BC B100–12); Lower Freilingen Beds, MTB Mechernich (BC B113–17); same stratigraphical level, MTB Münstereifel (BC B118–28). Freilingen Beds, MTB Dollendorf (BC B129); Freilingen Beds, Eilenberg Horizon, MTB Dollendorf (BC B130, 131); Givetian, Loogh Beds, Rech Horizon, Hillesheimer Syncline (BC B132, 133); Middle Devonian, Gerolstein (BM B39562, 3); Middle Devonian (BM B62946, B86023); Mitteldevon, *ostiolatus* Horizon, Geisdorf (SMF); Mitteldevon, Gerolstein (SMF). South-west England: Upper Devonian (probably Petherwin Beds, Gatehouse Quarry), Petherwin (GSM 34/20).

### *Schizophoria strigosa* (Sowerby)

Plate 66, figs. 8, 9, 11, 12; text-figs. 21, 22

1842 *Orthis?* *strigosa*, Sowerby, p. 409, pl. 38, fig. 7.

1886 *Orthis*; Maurer, p. 18.

1887 *Orthis strigosa* Sowerby; Béclard, p. 88, pl. 4, figs. 15, 16.

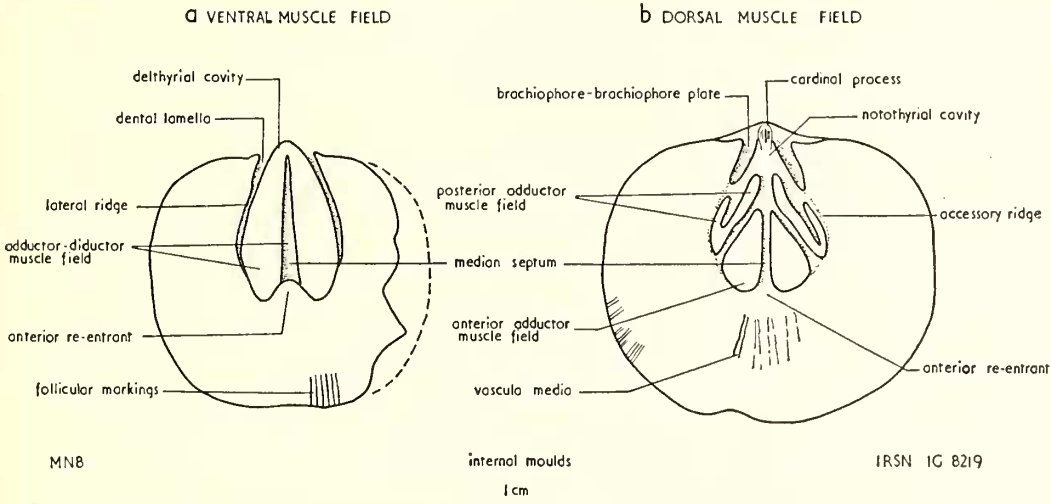
1893 *Orthis occulta* Maurer, p. 9, pl. 3, figs. 5–9.



non 1871 *Orthis strigosa* Quenstedt, pl. 56, figs. 55, 56.  
 non 1890 *Orthis personata* Zeiler; Kayser, pl. 2, figs. 3-6.

*Type.* Sowerby's specimen (1842) cannot be traced. This was collected from Devonian rocks of the Dill synclinorium. A neotype, a dorsal internal mould, has been selected from the Museum für Naturkunde, Berlin. This was collected from the Lower Devonian, Rauhflaserschichten, at Seifen.

*Diagnosis.* Shell medium to large, quadrate to elliptical. Ventral muscle field moderately long, flabellate, strongly incised, with narrow to broad, rounded median septum. Moderately thin brachiophores and brachiophore plates. Long peripheral follicular markings.



TEXT-FIG. 21. *Schizophoria strigosa* (Sowerby). Ventral and dorsal muscle fields.

*Description.* All specimens examined are preserved as internal moulds. Internal mould medium to large, dorsibinconvex, quadrate to elliptical, with greatest width at mid-length. Anterior commissure rounded uniplicate.

Ventral muscle field (text-fig. 21a) one-half to two-thirds valve length, flabellate, strongly incised. Shallow anterior re-entrant, or re-entrant absent (text-fig. 21a). Median septum varying in width, rounded, broadening, and increasing in height anteriorly.

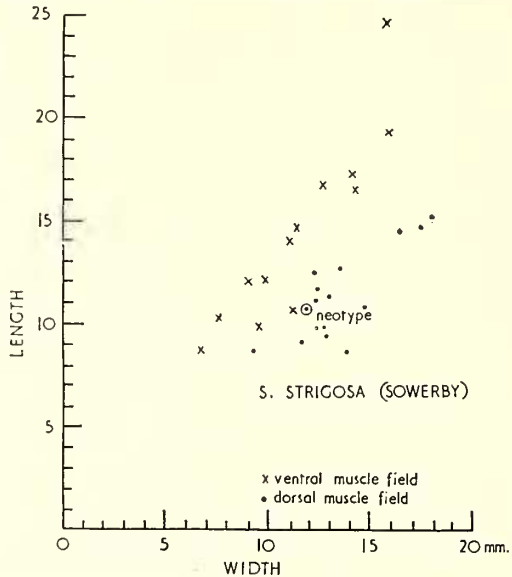
Cardinal process differentiated into oval myophore supported by narrower shaft. Myophore compound, with up to twelve lateral ridges. Dorsal muscle field (text-fig. 21b) incised, quadrate to rounded. Accessory ridges smoothly reflexed anteriorly to form shallow, sub-rounded anterior re-entrant. Median septum narrow, subangular, narrowing and decreasing in height anteriorly. Anterior adductor muscle scar pyriform; posterior adductor muscle scar bipartite, with longer inner lobe. Long follicular markings developed peripherally.

*Dimensions.* Dimensions of available muscle fields are plotted on text-fig. 22.

*Remarks.* Sowerby (1842, pl. 38, fig. 7) illustrated a fragmentary ventral internal mould, under *Orthis? strigosa*, from the Silurian of Haiger Sülbach (Dillenburg) in the German Rhineland. More recent work has shown that Devonian rocks outcrop in the Dill

synclinorium, and not Silurian rocks as previously supposed. Other German and Belgian material of this species is Lower Devonian in age. Béclard (1887, pl. 4, fig. 17) illustrated a similar ventral internal mould under *Orthis strigosa* Sowerby, from the Dinant Basin, Belgium.

Detailed and accurately localized collections from the Lower Devonian of Belgium (deposited in the Institut royal des sciences naturelles) include forms closely resembling Sowerby's, Béclard's, and Maurer's illustrations. These have been listed under *S. strigosa* (Sowerby). The dorsal muscle fields of these specimens (text-fig. 21b) closely



TEXT-FIG. 22. Dimensions of muscle fields of *Schizophoria strigosa* (Sowerby).

resemble Maurer's illustrations. But the ventral muscle field is often less flabellate, and the median septum narrower, as shown by Sowerby.

The ventral field occasionally resembles that of *Schizophoria vulvaria* (Quenstedt) in outline and narrow median septum. These variations have previously been illustrated by authors with specimens under *S. vulvaria* (eg. Oehlert 1887, pl. 5, figs. 1, 5) and *S. provulvaria* (Drevermann 1904, pl. 30, fig. 20). These could possibly belong to *S. strigosa*. The specimens of *S. vulvaria* illustrated by Oehlert (1887) have also been listed by Maillieux (1936, p. 53) under *S. provulvaria*, indicating further the presence of specimens with close similarities with both *S. provulvaria* and *S. vulvaria*.

The specimens illustrated by Drevermann (1904, pl. 31, figs. 16–18) under *S. provulvaria* have long follicular markings, characteristic of *S. strigosa*. Those of *S. provulvaria* are shorter.

*Schizophoria strigosa* appears in the Siegenian, and ranges into the lower Emsian, where it is succeeded by *S. vulvaria*.

Maurer (1893, p. 10, pl. 3, figs. 5–9) described and illustrated another species, *Schizophoria occulta*, which is here considered synonymous with *S. strigosa*. The ventral muscle fields and follicular markings are similar. Maurer also illustrated a dorsal

internal mould, not shown by Béclard or Sowerby. Maurer recognized *S. occulta* (i.e. *S. strigosa*) as distinct from the contemporaneous species *S. provulvaria*. The ventral muscle field of *S. occulta* is strongly incised, flabellate, with a rounded median septum, while that of *S. provulvaria* is much more strongly incised, protuberant in profile, and often with a broader median septum.

There are distinct differences in the dorsal muscle fields of *S. occulta* (*S. strigosa*) and *S. provulvaria*. The more slender brachiophores and brachiophore plates, and longer inner lobe of the digitate posterior adductor muscle scar, contrast with the strong brachiophores and brachiophore plates and more equal lobes of *S. provulvaria*.

*Material.* Belgium, Dinant Basin: Siegenien, Grauwacke de Petigny, Sg 3b (Hersdorferschichten), (IRSN IG8254); Grauwacke de Petigny, Sg 4 (IRSN IG8190); Grauwacke de Saint-Michel, Sg 3 (IRSN IG8219); Emsien Inférieur, Grauwacke de Pesche, Em 1a (IRSN IG8791). Germany: Siegener Schichten (MNB.B102.1—neotype), Rauhflaserschichten (MNB), Seifen, Lower Coblenzian (SMF).

### *Schizophoria vulvaria* (Quenstedt) 1867

Plate 66, figs. 13a, b; text-figs. 23–25

- 1655 *Hysterolithus*; Worm, p. 83, text-fig. on same page.  
 1719 *Hysterolithus*; Wolfart, pl. 3, figs. 3, 5, *non* 4.  
 1763–4 *Hysterolites vulva marina*; Baumer, p. 327, fig. 28.  
 1768 *Hysterolites*; Walch, p. 90, pl. B4, figs. 5, 6.  
 1820 *Hysterolites vulvarius* Schlotheim, p. 247, pl. 29, fig. 26? *non* 2a, 3.  
 1853 *Orth. Beaumonti* de Verneuil; Schnur, p. 215, pl. 37, fig. 9.  
 1867 *Hysterolithes vulvarius* Quenstedt, p. 577, pl. 49, fig. 2.  
 1868–71 *Hysterolithus vulvarius*; Quenstedt, p. 565, pl. 56, figs. 2–6.  
 1882 *Hysterolithes vulvarius*; Quenstedt, p. 737, fig. 252.  
 1885 *Hysterolithes vulvarius*; Quenstedt, pl. 57, fig. 13.  
 1887 *Orthis (Hysterolithes) vulvarius* Schlotheim sp.; Oehlert, p. 53, pl. 5, figs. 1–9.  
 1889 *Orthis hysterita* Gmelin; Kayser, p. 53, figs. 1, 7–9.  
 1893 *Orthis vulvaria* Quenstedt; Maurer, pl. 4, figs. 1, 2.

*non* 1753 *Hysterolithus*; Tessin, p. 90, pl. 5, fig. 2.

*non* 1850 *Orthis Beaumonti* de Verneuil, p. 180, pl. 4, fig. 8.

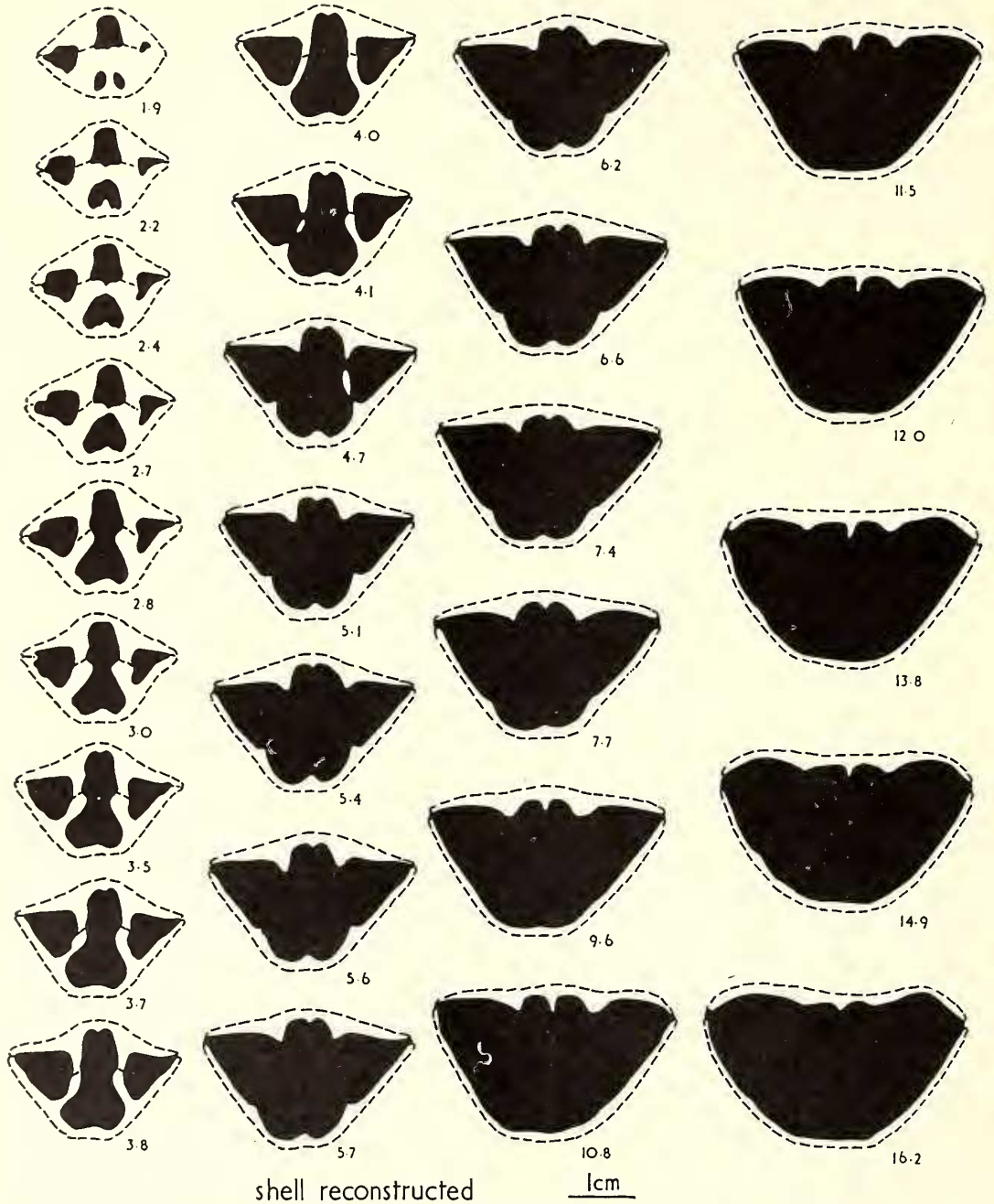
*non* 1938 *Schizophoria vulvaria* (Schlotheim); Comptes, p. 13, pl. 1, figs. 2, 3.

*Type.* Schlotheim's specimens (1820, pl. 29, figs. 2a, 3, and possibly 2b) were probably spiriferids (see 'Remarks'). Quenstedt (1867, 1868–71, 1882, 1885) is apparently the first author to describe and illustrate *Schizophoria vulvaria* proper. These specimens are deposited in the Geological Museum, Tübingen.

*Diagnosis.* Shell large, quadrate to rectangular. Ventral muscle field long, lanceolate to weakly flabellate, strongly incised, divided by narrow, subrounded median septum. Strong divergent brachiophore plates. Each posterior adductor muscle scar tripartite or quadripartite.

*Description.* Internal mould large, dorsibiconvex, quadrate to rectangular, with greatest width at or slightly anterior to mid-length. Anterior commissure rounded uniplicate.

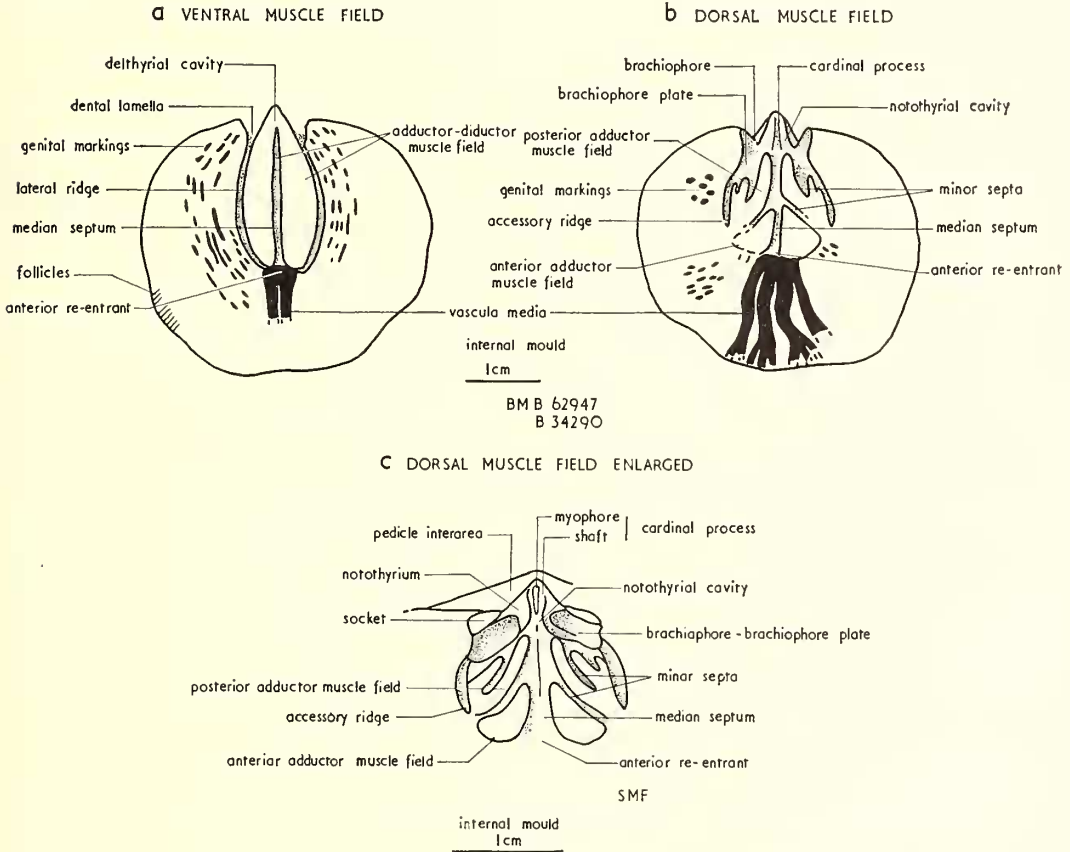
Ventral muscle field (text-fig. 24a) long, one-half to two-thirds valve length, lanceolate to weakly flabellate, strongly incised. Dental lamellae ventrally convergent anteriorly divergent. Shallow, subangular re-entrant, or re-entrant absent (text-fig. 24a). Median septum narrow, subrounded, broadening slightly anteriorly, first increasing, then decreasing in height (text-fig. 23, sections 3.5–16.2). Two sub-parallel vascula media, with lateral branches, originating from diductor muscle field or anterior re-entrant. Genital



TEXT-FIG. 23. *Schizophoria vulvaria* (Quenstedt). Transverse serial sections of plaster internal mould (BM B23179).

markings arranged concentrically, developed laterally and postero-laterally (text-fig. 24a).

Cardinal process prominent, broad myophore supported by narrower shaft (text-fig. 24c). Myophore compound, with up to six lateral ridges. Stubby brachiophores fused to strong, divergent brachiophore plates (text-fig. 23, sections 2.2-4.1). Dental sockets deep, oval.



TEXT-FIG. 24. *Schizophoria vulvaria* (Quenstedt). Ventral and dorsal muscle fields.

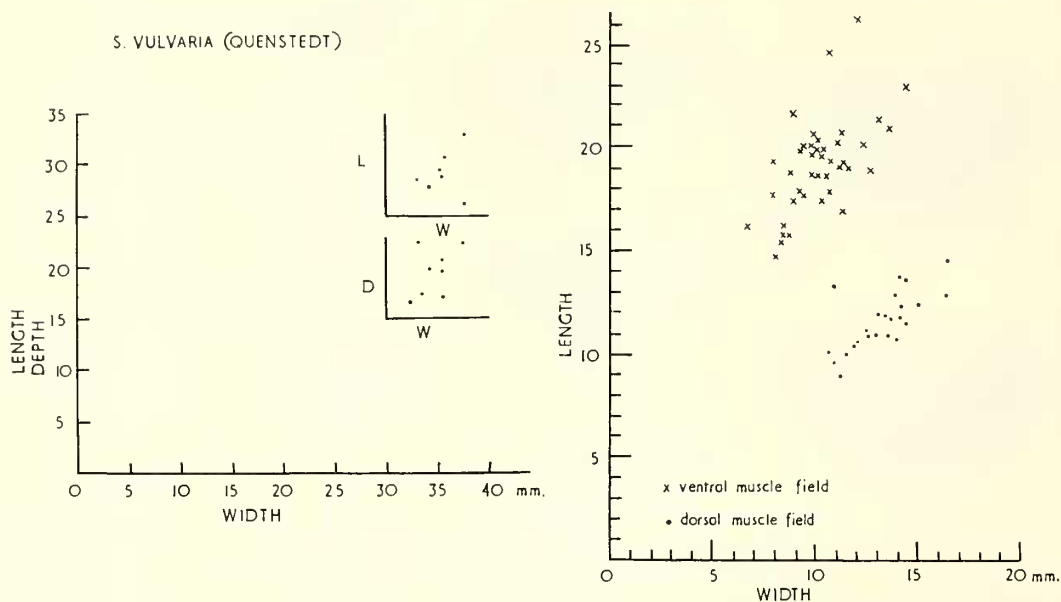
Dorsal muscle field (text-fig. 24b, c) quadrate to rounded, length and width approximately equal. Accessory ridges smoothly reflexed to form shallow, subrounded anterior re-entrant. Median septum low, broad, rounded, decreasing in height and narrowing anteriorly (text-fig. 23, sections 2.2-9.6). Anterior adductor muscle scar pyriform; posterior muscle scar generally tripartite or quadripartite, with longer inner lobe, shorter middle lobe(s), short outer lobe (text-fig. 24b, c). Two main divergent vascula media, each bifurcating, branching peripherally; two lateral vascula myaria occasionally developed from anterior adductor scars. Genital markings developed laterally and postero-laterally (text-fig. 24b). Short peripheral follicular markings (text-fig. 24a).

*Dimensions.* External dimensions and dimensions of available muscle fields are plotted on text-fig. 25.

*Remarks.* All the specimens examined are preserved as internal moulds.

Comparisons with *Schizophoria strigosa* (Sowerby), *S. provulvaria* (Maurer), and *S. striatula* (Schlotheim) are made under these species. *Schizophoria strigosa* and *S. provulvaria* range from the Sigenian to Lower Emsian. *Schizophoria vulvaria* appears higher in the Emsian, ranging into the Lower Eifelian, when it is succeeded by *S. striatula*.

Maillieux (1932, p. 24) presented a long synonymy of *S. vulvaria*, and discussed the naming of the species, with reference to authors of the seventeenth century. The name



TEXT-FIG. 25. Dimensions of *Schizophoria vulvaria* (Quenstedt).

*S. vulvaria* is synonymous with *Hysterolites*. Gmelin (1790, p. 3345) very briefly described a form under *Anomia hysterita*, which has been included under *S. vulvaria* by later authors. However, this description is not specific.

Schlotheim (1820, p. 247, pl. 29, figs. 2, 3), the stated author of the species by Quenstedt and later authors, described and illustrated some specimens grouped under *Hysterolites vulvarius*, which have the transverse outline and long hinge-line characteristic of a spiriferid. His figure 2*b* has a lanceolate ventral muscle field characteristic of *S. vulvaria*, but the hinge-line is curved, obscuring its length. The mould outline and muscle form of figure 2*b* also probably represents a spiriferid.

Later authors have apparently misinterpreted Schlotheim's work as actually representing the schizophoriid species *S. vulvaria*, mainly on the basis of the ventral muscle field in his figure 2*b*.

Quenstedt (1868-71 p. 565) stated that Schlotheim (1820, pl. 29, figs. 2*a*, 3) incorrectly described and figured specimens under *S. vulvaria*, and that only figure 2*b* could possibly represent the ventral valve of *S. vulvaria*. However, Schlotheim makes no reference to the genus *Schizophoria* (then *Orthis*) in his description, and was probably describing a

new spiriferid, since *Hysterolites* is an old group term for spiriferids. He described the specimens under *Hysteroliten*.

The ventral muscle field of Schlotheim (1820, pl. 29, fig. 2*b*) has confused later authors, who incorrectly recognized Schlotheim as author of the schizophoriid species *S. vulvaria*. Quenstedt (1867, 1868–71, 1882, 1885) was the first author to describe and illustrate *S. vulvaria* as such. Quenstedt is hereby listed as the author of *S. vulvaria*.

De Verneuil (1850, p. 180, pl. 4, figs. 8*a–d*) described and illustrated a new species *Orthis Beaumonti* from the Devonian of northern Spain, which resembles *S. vulvaria* in shell outline, and elongate form of the ventral muscle field. But the ventral valve pallial sinus and genital markings of *O. Beaumonti* are radially arranged, in contrast to the concentric arrangement in *S. vulvaria*. In the dorsal valve of *O. Beaumonti*, the anterior adductor muscle scars are very small, the posterior scars apparently non-digitate, and only two parallel *vascula media* originate from the anterior of the muscle field. In *S. vulvaria*, the anterior muscle scar is larger, the posterior scar tripartite or quadripartite, and four to six trunks diverge from the muscle field.

Compte (1938 p. 13, pl. 1, figs. 2, 3) described and illustrated specimens from the Lower and Middle Devonian of northern Spain under *S. vulvaria*, with *Orthis Beaumonti* de Verneuil listed in synonymy. Compte's specimens resemble those of Verneuil, and were collected from the Upper Siegenian, Emsian, and Lower Eifelian stages. *Schizophoria vulvaria* from Belgium and Germany is restricted to the Emsian and Lower Eifelian stages.

Although resembling and probably related to *S. vulvaria*, *Orthis Beaumonti* has not been listed in synonymy with *S. vulvaria*, but is here considered a separate form, based on its dorsal muscle field and pallial sinus markings.

*Material.* Belgium, Dinant Basin; Lower Devonian (BM B15708). Emsien Supérieur, Grauwacke de Hierges, Em 3 (IRSN IG4916, 5391, 5746, 5910, 5911, 8254, 8284, 8573); Couvinien Inférieur, Assise de Bure (CO 1)–CO 1a (IRSN IG12409), CO 1b (IRSN IG5746); Germany, Lower Devonian (BM B19002) Lahnstein; (BM B23179, B34290, B49920, B39450) Eifel; (BM B39435) Coblenz; (BM B86626, 7), mouth of River Lahn; Ober Coblenzian (HMUG L2031) Daleiden; Coblenzian (HMUG L5344) Grimbach; Ober Ems (SMF) Prüm.

#### PHYLOGENY

The postulated phylogeny of Devonian species of *Schizophoria* studied, and possible links with the Carboniferous, is shown on text-fig. 26. This chart is based solely on material examined, and could conceivably represent only a part of the true picture of descent.

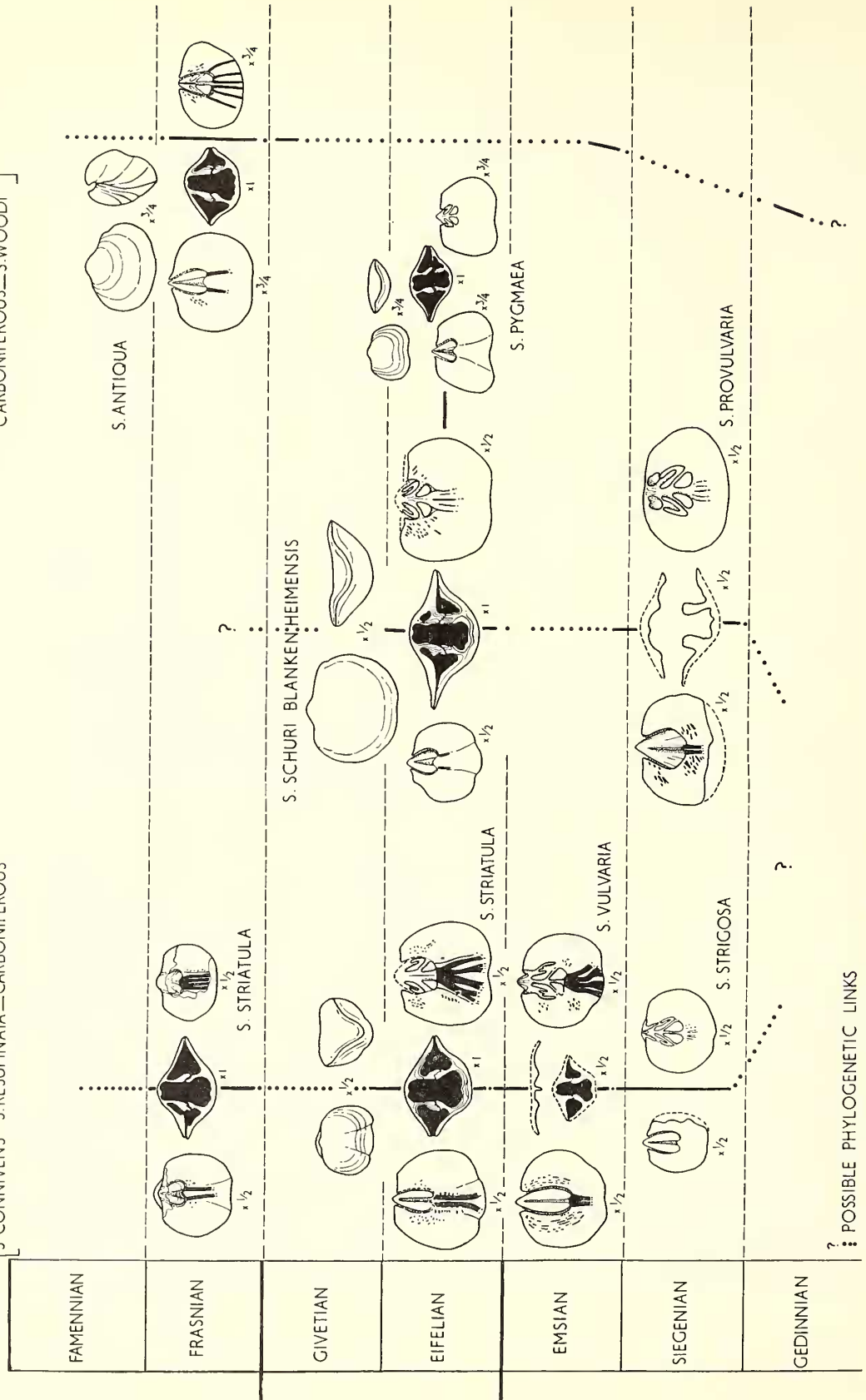
The relationship of species has been based externally on outline, and internally on muscle field patterns and form of the brachiophore plates, correlated with stratigraphical occurrence. External and internal features are illustrated on text-fig. 26.

The species appear to have been derived from two, perhaps three, root stocks. *Schizophoria antiqua* (Gedinnian–Frasnian) is the first species to appear in Europe. Morphologically, *S. antiqua* bears little relationship to other Devonian species, but resembles more closely *S. woodi* from the Carboniferous. *Schizophoria antiqua* is represented as a separate line of development.

Other Devonian species could have been derived from the *S. provulvaria* (Siegenian–Emsian) and *S. strigosa* (Siegenian–Emsian) stocks. *Schizophoria provulvaria* appears to have given rise to *S. pygmaea* and *S. schuuri blankenheimensis* (Eifelian). There are close resemblances in external outline and muscle field patterns. Although *S. pygmaea* is

[ S. CONNIVENS S. RESUPINATA—CARBONIFEROUS ]

CARBONIFEROUS—S. WOODI ]



TEXT-FIG. 26. Postulated phylogeny of *Schizophoria* from the Devonian of western Europe.